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# Watershed-scale patterns of seaward migration in *Lentipes concolor*, a Hawaiian stream goby

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**WATERSHED-SCALE PATTERNS OF SEAWARD MIGRATION IN  
*LENTIPES CONCOLOR*, A HAWAIIAN STREAM GOBY**

A Dissertation  
Submitted to the Graduate Faculty of the  
Louisiana State University and  
Agricultural and Mechanical College  
in partial fulfillment of the  
requirements for the degree of  
Doctor of Philosophy

in

The Department of Biological Sciences

by  
Mark Gordon McRae  
B.S., Oregon State University, 1996  
M.S., Louisiana State University, 2001  
May 2007

## **DEDICATION**

To Robert E. McRae  
1933 –2006

A wonderful father

and

To Charles T. Chong  
1962 – 2005

An inspiration, colleague, and good friend

## ACKNOWLEDGEMENTS

First and foremost, I would like to thank my major professor, Dr. J. Michael Fitzsimons, for sharing his wealth of experience, knowledge, and wisdom with me, and for allowing me the freedom to design and pursue this project. He showed me how to be a better scientist and a better person. The members of my graduate committee, Drs. Donald M. Baltz, Kenneth M. Brown, C. Frederick Bryan, and W. James Catallo, have provided me with valuable encouragement and good advice throughout the course of my work at L.S.U. The Hawai'i Division of Aquatic Resources (DAR) provided the funding (United States Fish and Wildlife Service Sportfish Restoration Program Grant F-14-R-27) that made the research described in this dissertation possible. The entire Hilo-based DAR staff provided both logistical assistance and valued friendships as I worked on this research. Their commitment to responsible and effective stewardship of Hawaii's freshwater resources is exemplary. I would especially like to thank Dr. Robert T. Nishimoto for being a professional mentor and provider of moral support. Thanks also go to Darrell Kuamo'o for generously sharing his knowledge of Hawaiian stream fishes. Glenn Higashi, Lance Nishiura, Troy Shimoda, Tim Shindo, Troy Sakihara, and Grant Kow were always quick to lend a hand when I needed help in the field or in the lab. Charles T. Chong encouraged and inspired me to pursue a career in science over 20 years ago, and provided me with a great example of how to be an enthusiastic and creative stream ecologist. Dr. Daniel P. Lindstrom shared copies of his photographs that helped immensely with identification of larval gobies. Dr. Kim Bell showed me the value and feasibility of performing periodic regression analysis. Several of my fellow L.S.U. students assisted in the field. Lori Benson, Jessica Coleman, Thorpe Halloran, Pam MacRae, Cheryl Murphy, and Alison Styring were hard-working and cheerful helpers

during long, cold nights of drift sampling. A special acknowledgement and thank-you goes to my parents, Robert and Brenda McRae, who instilled in me the belief that, with God's help, all things are possible. When times were difficult, their endless encouragement and unconditional love provided me with the strength I needed to persevere. Finally, I extend a very special thank-you to my wife (and closest colleague), Lori Benson McRae for all of her patience, supportiveness, loving encouragement, and wonderful companionship.

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## ABSTRACT

The native stream fishes of the Hawaiian Islands are uniquely adapted to colonize and thrive in lotic habitats in this extremely isolated archipelago. Chapter 1 of this dissertation introduces the five native fishes of Hawaii's streams and describes the variety of lotic habitats they occupy. All five species have amphidromous life cycles, and, as such, their larvae must migrate to the ocean soon after hatching. Of the five species, *Lentipes concolor* is able to scale Hawaii's highest waterfalls during the migration back into fresh water, and therefore inhabits the widest variety of stream types. Adult *L. concolor* are found a few meters from the ocean in small streams that enter the ocean as terminal waterfalls. *Lentipes concolor* also inhabit inland stream reaches located at high elevations in large streams with low gradient terminal estuaries. This dissertation examined potential spatial and temporal patterns in the migration of newly hatched *L. concolor* larvae as they passively drifted from instream hatching sites to marine habitats. Results presented in Chapter 2 demonstrated that more larvae successfully completed seaward migration in terminal waterfall streams than did larvae spawned in the upper reaches of larger, higher-order streams. In Chapter 3, a significant diel drift pattern was observed during 24-hour sampling. Although larvae were captured in drift nets during both day and night, a preponderance of larvae during the first three hours following sunset was the most commonly observed trend. Results presented in Chapter 3 also suggest that in terminal-waterfall streams, spawning and therefore downstream movement of larvae occur more commonly during new-moon phases. A lack of distinct lunar periodicity in upland reaches of large streams is hypothesized to possibly be related to the high frequency and intensity of flash floods that may disrupt the sequence of courtship and spawning behavior of adult *L. concolor*. Chapter 4 discusses ways in

which the new information contained in the previous two chapters may change current paradigms regarding the population ecology and conservation of native stream fishes in Hawai‘i.



## **CHAPTER 1**

### **INTRODUCTION**

## Hawaiian Stream Fishes

The ancestors of Hawaii's indigenous stream fishes originally had to cross thousands of kilometers of open ocean to invade the extremely isolated freshwater habitats that exist in such a remote archipelago. This seemingly impossible feat occurred due to the fact that all five species of native stream fishes in Hawai'i are amphidromous and have a relatively lengthy marine larval phase which fosters dispersal (Radtke et al., 2001). Amphidromy is a form of diadromy, or a life cycle that is split between freshwater and marine environments (McDowall, 1992; Figure 1). Specifically, juvenile and adult fish live in freshwater habitats, which is where demersal spawning takes place. Newly hatched, or pre-marine (Font, 1996), larvae must passively drift downstream to their oceanic feeding sites. Once in the ocean, the larvae become a part of the pelagic zooplankton community until they mature into postlarvae (Radtke et al., 1988). Post-larvae must then migrate back into fresh water which is where they metamorphose rapidly into juveniles (Nishimoto & Kuamo'o, 1997; Schoenfuss et al., 1997). Due to this dependence on marine environments, none of the indigenous fishes that live in Hawaii's streams and rivers can be considered primary or secondary freshwater species (McDowall, 1997; Balon & Bruton, 1994). Indeed, in many respects, these fishes' life history characteristics are more similar to those for species which inhabit nearshore marine environments such as coral reefs and intertidal zones (Kinzie, 1993).

All five species are in the suborder Gobioidae, and are referred to collectively as 'o'opu. The endemic species *Lentipes concolor*, *Sicyopterus stimpsoni*, and *Stenogobius hawaiiensis*, as well as the indigenous *Awaous guamensis*, are in the family Gobiidae, while the endemic *Eleotris sandwicensis* is in the family Eleotridae (Figure 2). Congeners of all five native stream fishes can be found in streams on islands throughout

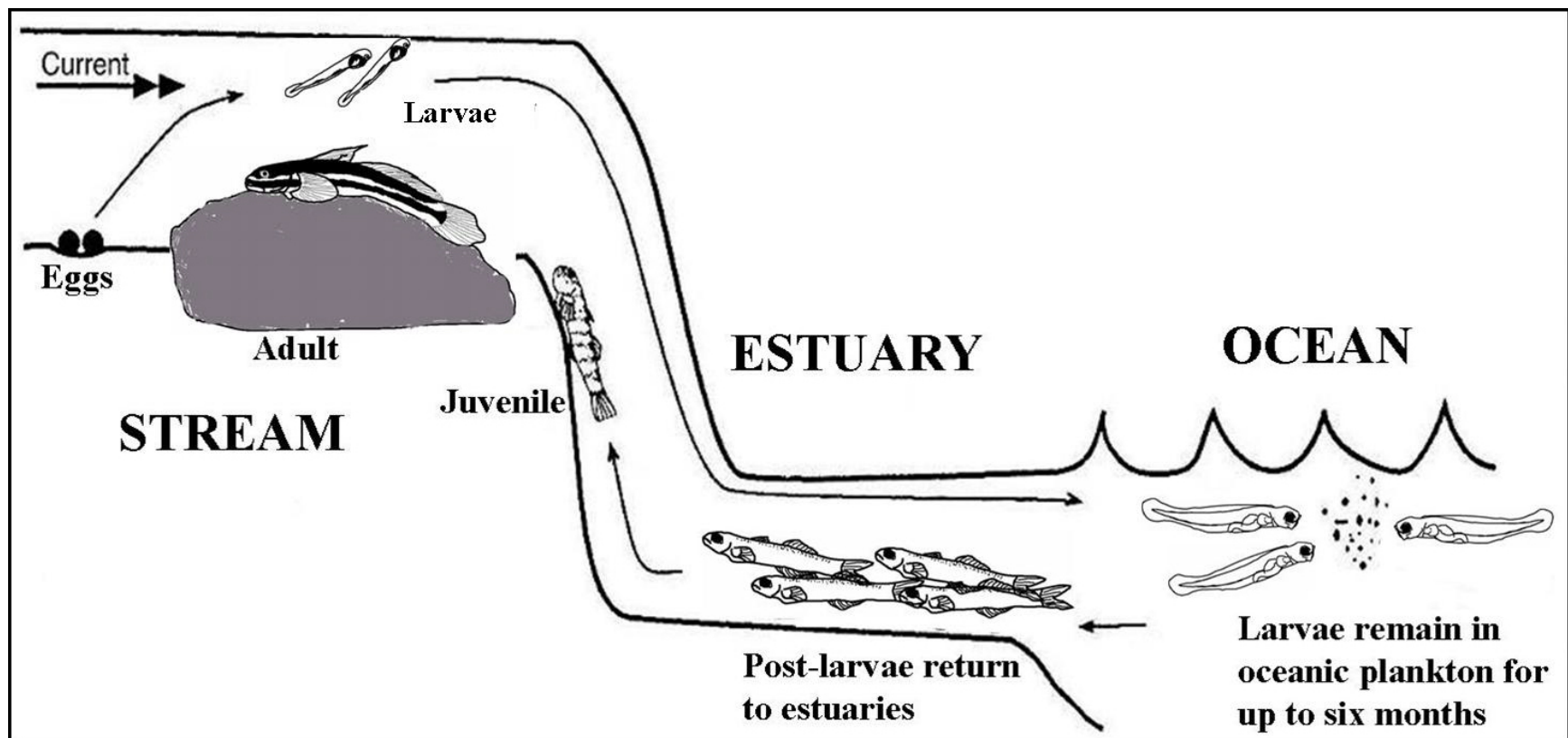


Figure 1. Diagram that depicts the amphidromous life-cycle of an amphidromous goby.

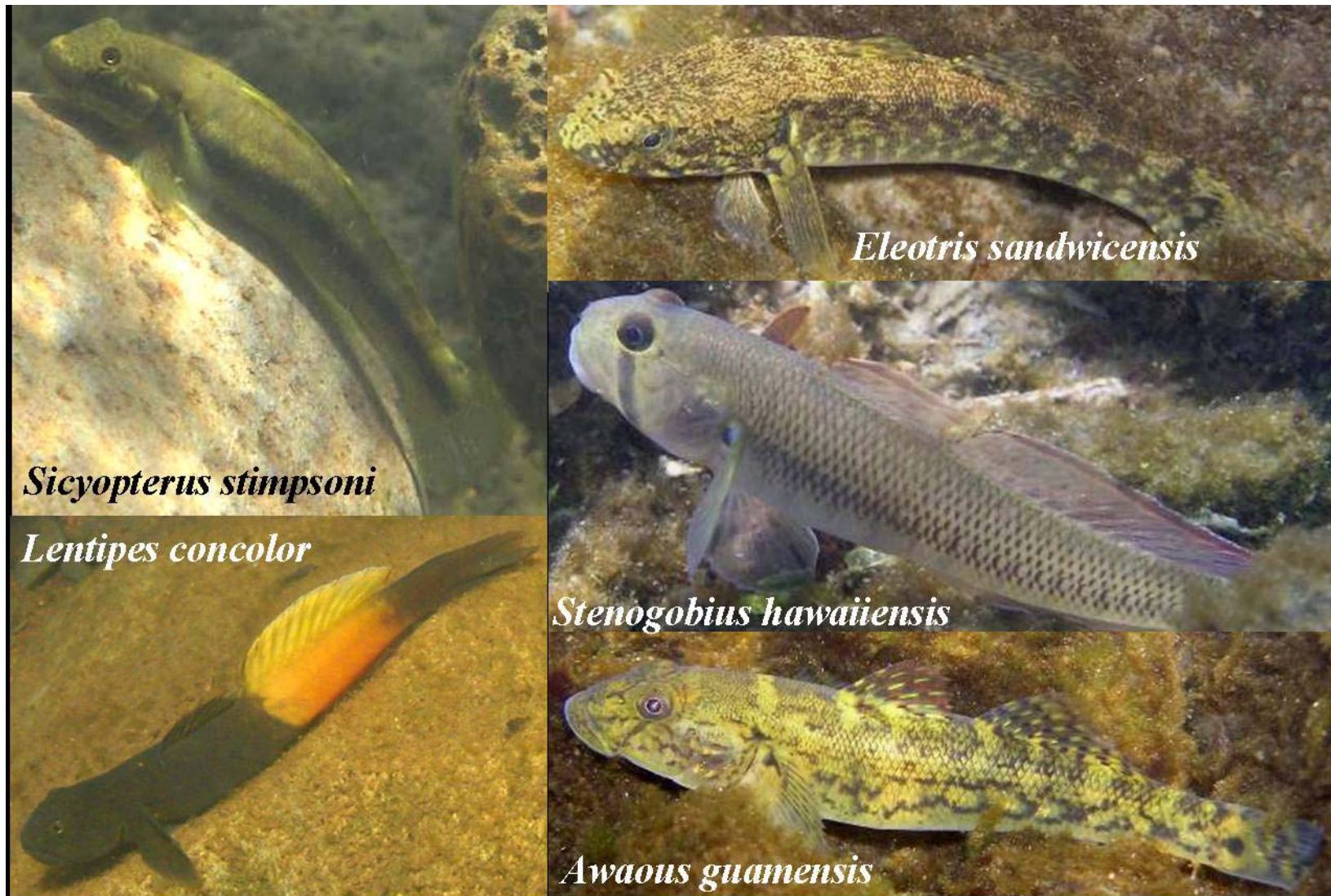


Figure 2. The five gobioid fishes native to Hawaiian streams. Photos by L.K. McRae.

the Pacific, and it is believed that 'o'opu evolved from amphidromous ancestors, native to other islands, whose pelagic marine larvae were advected by ocean currents to the newly formed Hawaiian Islands (McDowall, 2003).

The presence of a marine larval stage in amphidromous fishes not only enabled their original colonization of the Hawaiian Islands, it also facilitated the survival and evolution of these fishes in the highly unstable habitats present in Hawaiian streams (Fitzsimons et al., 1996). Streamflow in Hawai'i is characterized by frequent and intense flash floods that rise and fall dramatically in response to heavy rains on windward portions of the islands (Tomlinson & DeCarlo, 2003; Figure 3). It is the amphidromous life cycle that facilitates the persistence of these species in such high-disturbance environments. Natural restocking of streams with postlarval immigrants from the ocean maintains thriving populations of juveniles and adults in spite of potential mortality associated with catastrophic floods (Fitzsimons & Nishimoto, 1995). The geologically dynamic nature of the Hawaiian Islands also has the potential to devastate freshwater habitats. The presence of the marine larval phase has enabled amphidromous species to avoid the inevitable extinction that would befall landlocked fishes in streams destroyed by volcanism or erosion (McDowall, 1996; Schoenfuss et al., 2004).

### **Lotic Habitats in the Hawaiian Islands**

Polhemus et al. (1992) outlined a classification for continuous perennial stream reaches on islands in the tropical Pacific in which three main reach-type divisions were described from gradient, physico-chemical characteristics, and faunal composition. *Headwater reaches* were described as being high in elevation (> 800 meters) with high gradient (> 30%), and comprised mainly of bedrock. *Midreach* areas are generally between 50 and 800 m in elevations, between 5 and 30% gradient, with substrata predominantly





Figure 3. Flash flood in lower Umauma Stream, April 2004.

composed of boulders, cobble, and gravel. *Terminal reaches* were defined as “watercourses below sharp gradient that bars upstream migration of itinerant marine fishes” (Polhemus et al., 1992). Elevations in terminal reaches are usually <50m and gradients <5%, with substrata that consist mainly of cobble, gravel, sand, and sediment. In Japan, Mizuno & Kawanabe (1981) outlined a topographically based classification system for stream reaches which defines reach types by two topographic criteria. The first criterion is the number of riffle/pool sequences in stream segments between meander bends. Type “A” reach types have more than one riffle/pool sequence between bends, while Type “B” reaches have only one. The second criterion relates to the gradient and turbulence of riffles or cascades connecting the pools. Type “a” are waterfalls, Type “b” are turbulent, high-gradient riffles or cascades, and Type “c” are smooth, low-gradient riffles. Thus, a steep reach having two or more plunge pools separated by waterfalls in each segment between meander bends would be designated as Type Aa (Figure 4), whereas a reach of moderate gradient with only one pool and turbulent riffle between bends would be Type Bb. Reaches designated as Aa are typically found in first order streams that flow down steep slopes. Type Bc reaches are commonly found flowing through coastal plains and are low gradient and relatively sinuous. Mizuno & Kawanabe’s (1981) finer-scaled classification system will be used, along with the broader-scale classification of Polhemus et al. (1992), to describe the range of stream and reach types that amphidromous fishes inhabit in the Hawaiian Islands.

Two stream types were described by Nishimoto & Kuamo‘o (1991), and they represent the extremes in a spectrum of stream morphologies which range from short, first order streams with low discharge and high gradients to relatively long, high discharge, second or third order streams with extended, low gradient terminal reaches that





Figure 4. Midreach of Umauma Stream, Island of Hawai'i, demonstrating an example of "Aa" topography.



form estuaries near the stream mouth. Even though both extremes exist on all five of the Hawaiian Islands that have perennial streams, on the geologically younger islands such as Hawai‘i and Maui, short, steep, straight streams are the most common type (Nishimoto & Kuamo‘o, 1991). In these small streams, Type Aa reaches extend from the stream-mouth up to the headwaters. These small freshwater systems have an abundance of waterfalls, cascades, and plunge pools with the stream often entering the ocean as a terminal waterfall – the stream falls off the edge of a cliff directly into the ocean or onto a narrow rocky beach (Figure 5). Streams of this type will be referred to hereafter as “terminal-waterfall streams” (Nishimoto & Kuamo‘o, 1991). On the relatively older islands such as O‘ahu and Kaua‘i, larger stream systems are more common than they are on the younger islands. Long, low gradient terminal reaches exist upstream of sinuous mixohaline estuaries (Nishimoto & Kuamo‘o, 1991), above which are long midreach areas dominated by Type Bc and Type Bb reaches that gradually transition into Aa-Bb reaches farther inland. Type Aa reaches are encountered in these “estuary streams” (Nishimoto & Kuamo‘o, 1991) in upper midreach and headwater areas that can be several kilometers inland from the mouth of the stream (Figure 6).

### **Instream Distributions of Hawaiian Amphidromous Gobies**

The distributions of amphidromous fishes in Hawaiian streams are strongly influenced by each species’ ability to disperse above high gradient and vertical stream features (i.e., cascades and waterfalls) on their return migration from the ocean (Nishimoto & Kuamo‘o, 1997). Postlarvae and juveniles of three of the five species have the ability to climb the vertical rock faces associated with waterfalls by using pelvic fins fused into a suction disk (Figure 7). *Eleotris sandwicensis* lacks fused pelvic fins while *S. hawaiiensis* has fused pelvic fins, but lacks the associated musculature necessary



Figure 5. Terminal waterfall at the mouth of Manoloa Stream on the Island of Hawai'i.



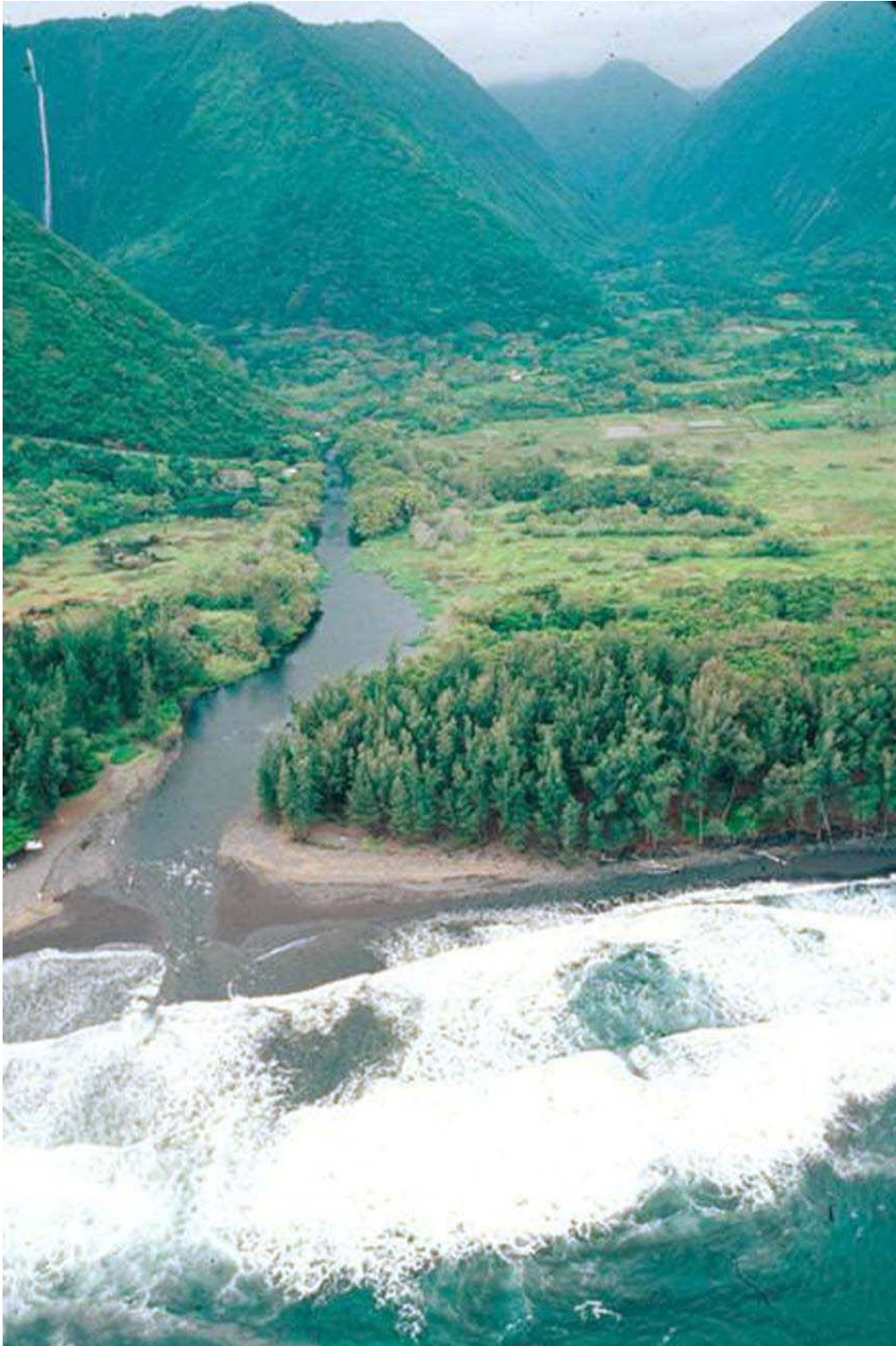


Figure 6. Example of an estuary stream. Wailoa Stream, Waipi'o Valley, Island of Hawai'i. Photo by D.G.K. Kuamo'o.

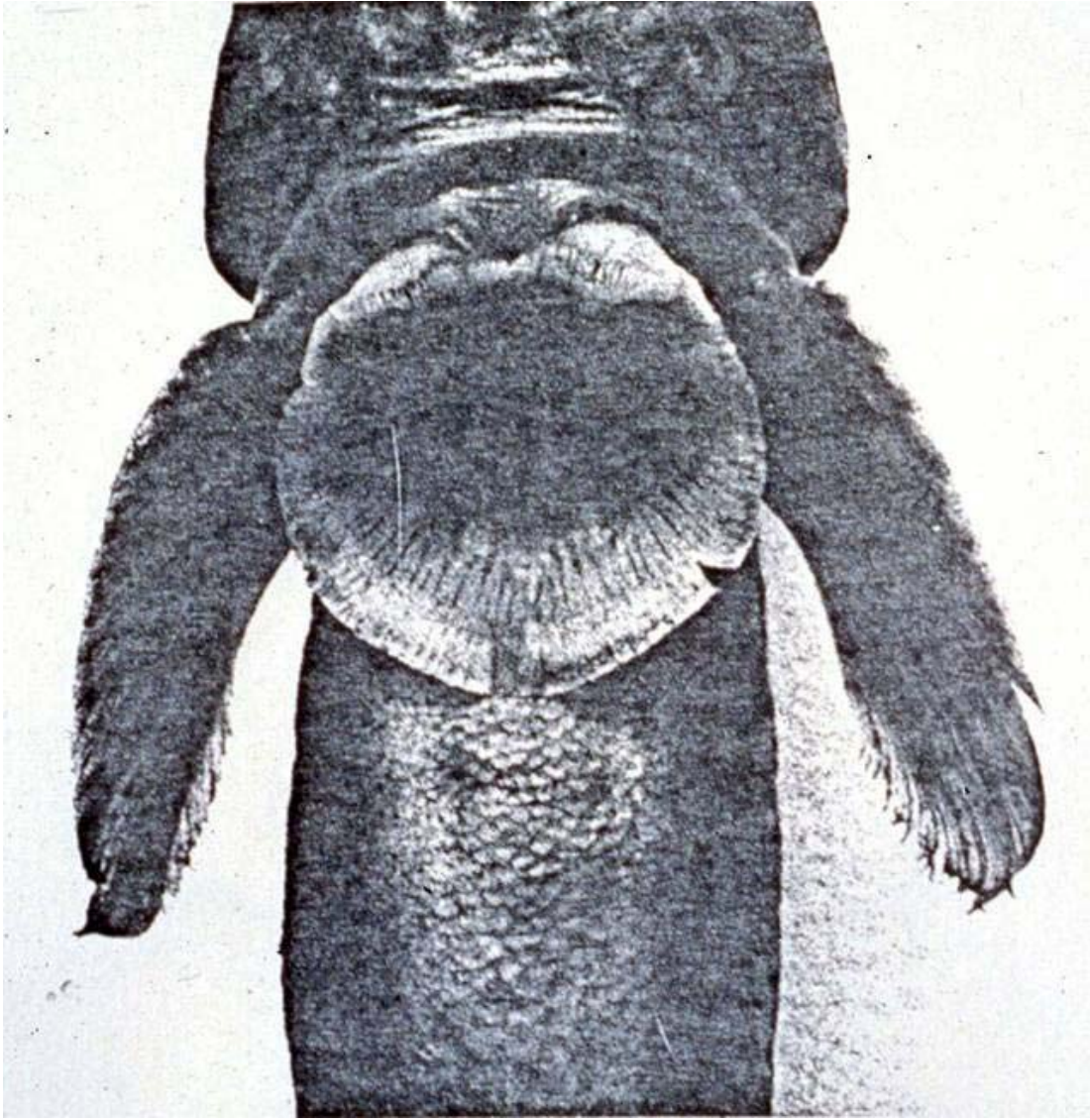


Figure 7. Fused pelvic fins of an adult *Sicyopterus stimpsoni*. Photo by M.T. Tomihama.

for climbing waterfalls (Nishimoto & Kuamo‘o, 1997). Both of these species, therefore, are precluded from dispersing upstream of any precipitous waterfall and are restricted in their distributions to terminal reaches and estuaries (Fitzsimons & Nishimoto, 1995).

*Awaous guamensis* and *S. stimpsoni* can climb and disperse beyond moderately high waterfalls (less than ~20 m) (Fitzsimons & Nishimoto, 1990) and are found in Type Bc, Bb, and Aa mid and terminal reaches. Vertical waterfall height does not appear to be a limiting factor for *L. concolor* as they migrate upstream towards their adult habitats.

Adult *L. concolor* have been observed in stream reaches located at elevations higher than 1 km (Fitzsimons & Nishimoto, 1990) and in stream reaches that were located above a waterfall with a more than 300 m vertical height (Englund & Filbert, 1997).

Due to the fact that the instream distributions of the five amphidromous Hawaiian gobioids are largely determined by their waterfall-climbing ability, it follows that these distribution patterns will vary with the type of stream they invade when returning to fresh water from the sea (Nishimoto & Kuamo‘o, 1991). In large streams with terminal estuaries, it is common to find juveniles and adults of all five species, with *E. sandwicensis* and *S. hawaiiensis* occurring in the estuary, terminal reach and lower midreach areas. *Awaous guamensis* and *S. stimpsoni* are common in the upper regions of the terminal reach, and in midreach areas, while *L. concolor* typically occurs farther upstream, in the upper midreaches (Figure 8). In these estuary streams, *L. concolor* appear to migrate inland until they encounter their preferred Type Aa habitats and are therefore often located farther inland than any of the other species (Kinzie, 1988; Nishimoto & Kuamo‘o, 1991; Kido et al., 2002). Similar distribution patterns have been described for assemblages of diadromous fishes in streams in Micronesia (Parham, 1995; Nelson et al., 1997).

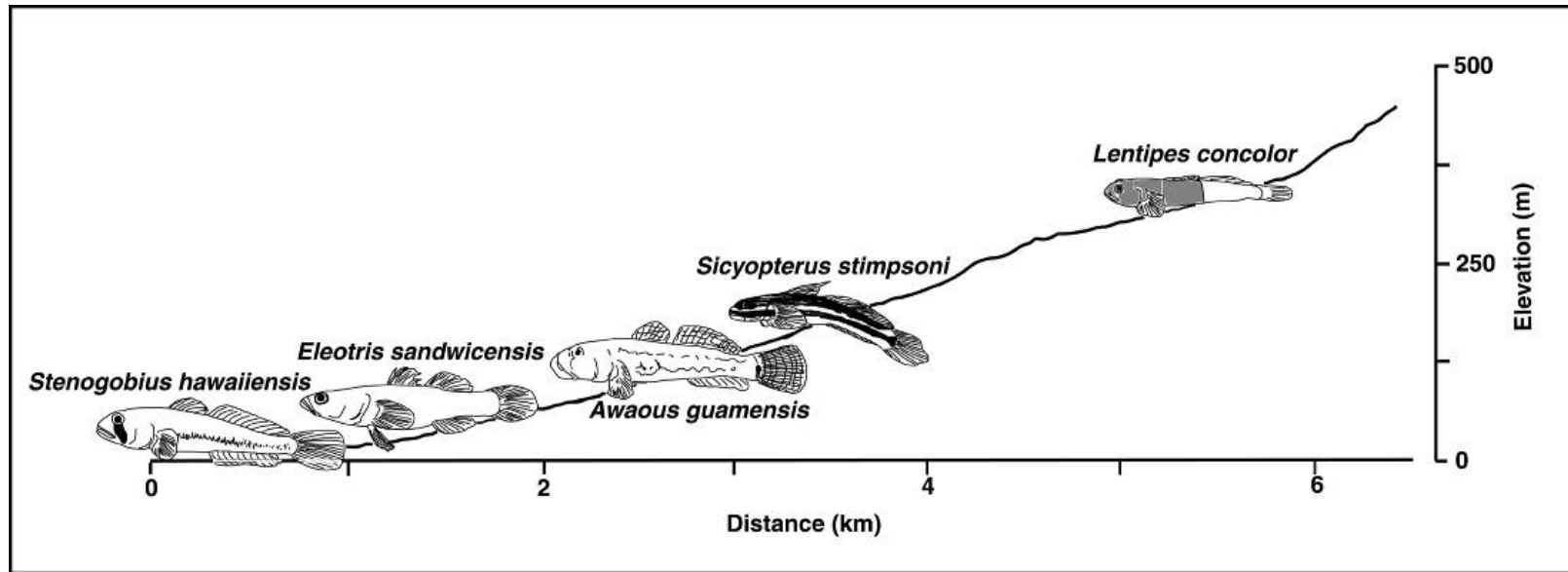


Figure 8. Elevational profile of Hakalau Stream that depicts the instream distribution of native fishes in an estuary stream. Adapted with permission from Nishimoto & Kuamo'o (1991).

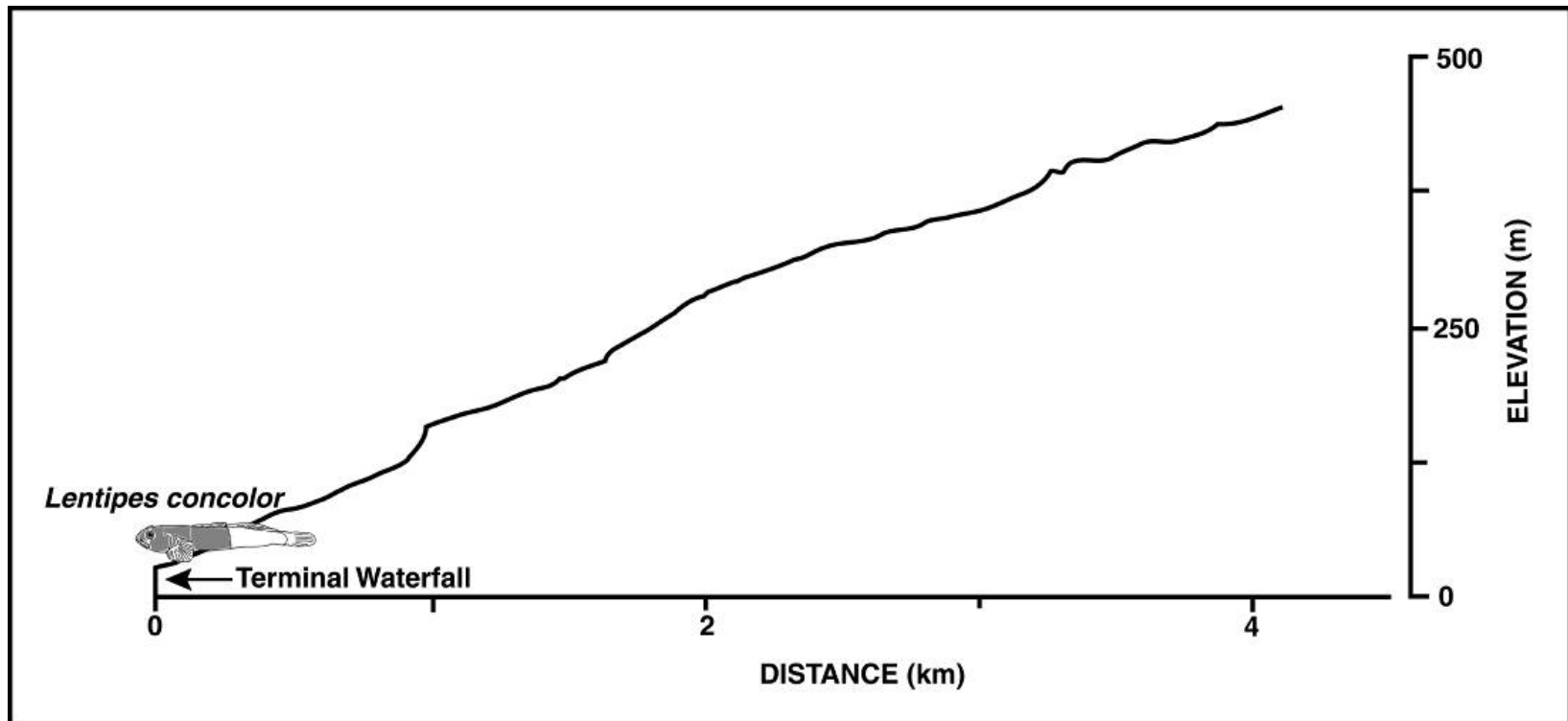


Figure 9. Elevational profile of a terminal-waterfall stream (Manoloa Stream). Adapted with permission from Nishimoto & Kuamo'o (1991).



At the other end of the size spectrum, Hawaii's smallest streams have a similar, albeit truncated, pattern of species distribution. In terminal-waterfall streams, the two non-climbing species, *E. sandwicensis* and *S. hawaiiensis* are either absent or are restricted to the short stretch of stream at the base of the terminal falls (Nishimoto & Kuamo'o, 1991). Depending on the height of the falls, the number of species that occur upstream of terminal waterfalls ranges from one to three. Because of their climbing ability, *A. guamensis*, *S. stimpsoni*, and *L. concolor* are able to disperse to areas upstream of the terminal falls. Upstream of the highest terminal falls, *L. concolor* can be the only species present, and they often occur in high densities a relatively short linear distance from the mouth of the stream (Figure 9), presumably because newly recruited individuals encounter their preferred adult habitat soon after they arrive at the top of the falls.

The abundance and frequency of occurrence of *S. hawaiiensis*, *E. sandwicensis*, *A. guamensis*, and *S. stimpsoni* generally decreases with increasing distance inland, as is the case for most species of amphidromous fishes (McDowall, 1996). In small terminal-waterfall streams, this pattern holds true for *L. concolor* as well. In large, higher-order streams, however, *L. concolor* typically do not inhabit low elevation sites in estuaries or nearshore midreaches (Nishimoto & Kuamo'o, 1991). Indeed, the largest populations of adult *L. concolor* are often found at high elevations, several kilometers from the ocean in Aa reaches located in the upper portions and inland tributaries of estuary streams.

Due to the fact that streams with terminal waterfalls are typically small first-order systems, the total amount of habitat available to adult *L. concolor* is typically much less than is present in the multiple tributaries and long upper midreaches of estuary streams. As such, although population densities may be very high in the short coastal reaches of terminal-



waterfall streams, the total numbers of adult *L. concolor* are usually much lower than they are in the larger drainages.

When one considers the variety of natural and anthropogenic stream features that may impede larval *L. concolor* as they move towards the ocean, it becomes apparent that factors that potentially affect the pre-marine larval stage may have strong effects on the overall population dynamics of this endemic species (Font, 1996). Because adult *L. concolor* spawn a few meters away from the ocean in small, terminal-waterfall streams, and several kilometers away from the ocean in the upper reaches of estuary streams, there are potentially strong differences in the challenges faced by larvae needing to reach the sea in these two stream types.

The goal of this dissertation was to document the existence of patterns in the seaward movement of pre-marine *L. concolor* larvae in both terminal-waterfall and estuary streams. Chapter 2 describes a study that compared these two different stream types with respect to the number of larval *L. concolor* that successfully completed their seaward migrations. Results presented in Chapter 2 showed that larvae hatched in terminal-waterfall streams more consistently reached the ocean than did larvae hatched in the upper reaches of estuary streams. Temporal patterns in downstream drift of *L. concolor* larvae are described in Chapter 3 at both the diel and lunar scales. Peaks in the numbers of larval *L. concolor* migrating downstream were observed during the first three hours after sundown, and on days leading up to and following a new moon. The final chapter of this dissertation, Chapter 4, explores the implications of the results reported in the previous two chapters on the population ecology and conservation of this remarkable species.

## **CHAPTER 2**

### **SPATIAL PATTERNS IN THE MIGRATION OF NEWLY HATCHED *LENTIPES CONCOLOR***

## Introduction

The entire assemblage of native gobioid fishes that inhabit lotic environments in the Hawaiian Islands is migratory – they move between freshwater and marine environments and can be classified specifically as freshwater-amphidromous (McDowall, 1988). The four gobies and one eleotrid that make up Hawaii's amphidromous ichthyofauna inhabit fresh water during their juvenile and adult phases. Demersal spawning takes place in streams, and, after hatching from eggs laid in nests located on the undersides of boulders (Kinzie, 1993), larvae are swept downstream towards the ocean, where they must arrive to access their planktonic food resources (Radtke & Kinzie, 1996). Larvae that successfully arrive at their marine habitats become part of the marine zooplankton community, remain in the ocean for several months (Radtke et al., 1988), and then must migrate back into streams as post-larvae, where they quickly metamorphose into juveniles (Schoenfuss et al., 1997).

The existing scientific evidence regarding the population structure of 'o'opu indicates that after the planktonic marine phase, postlarvae do not necessarily return to the streams in which they hatched. None of the native fishes are endemic to a single island. Genetic studies have discovered little or no genetic structuring among populations of 'o'opu from different islands in the Hawaiian archipelago and indicate that, at least to some degree, there exists for 'o'opu a single panmictic gene pool (Chubb et al., 1998; McDowall, 2003).

In general, the abundance and frequency of occurrence of 'o'opu in Hawai'i declines with increasing elevation and distance upstream from the sea (Nishimoto & Kuamoo, 1991; Kido et al., 2002), a pattern observed in most amphidromous fishes around the world (McDowall, 2000). *Lentipes concolor* is the one species that has instream distribution patterns that do not hold to this generality. In many of Hawaii's larger streams, adult *L. concolor* are more abundant in high elevation headwater reaches than they are in the more

coastal segments of the same stream (Nishimoto & Kuamo‘o, 1991). This somewhat unique distributional pattern can be attributed to at least two factors: 1) the remarkable ability of *L. concolor* to climb waterfalls and 2) their tendency to inhabit small, low-order stream reaches (Kinzie, 1988).

After returning to fresh water from the ocean, recruiting *L. concolor* are not prevented from climbing Hawaii's highest waterfalls (e.g., > 300m Hi‘ilawe Falls; Englund & Filbert, 1997). This remarkable climbing ability allows them to move upstream until they encounter their preferred habitats that are typically found in Aa stream reaches. The areas most often inhabited by *L. concolor* are relatively small, low order stream reaches that are high in gradient and have an abundance of large substrates such as boulders and bedrock (Kinzie, 1988). These types of reaches are found in streams that range in size from very small systems with terminal waterfalls that plunge directly into the ocean to relatively large rivers with long estuaries (Polhemus et al., 1992). *Lentipes concolor* inhabit both types of streams, with adults living in inland reaches in the larger streams, or in stream reaches that are very near to the ocean in small streams with terminal waterfalls (Nishimoto & Kuamo‘o, 1991). Due to the fact that estuary streams contain greater total amounts of their preferred habitats, some of Hawaii’s largest populations of adult *L. concolor* can be found in the upper reaches and first-order tributaries of these relatively large streams. Conversely, most terminal-waterfall streams in Hawai‘i are first-order systems that contain smaller total amounts of high-quality habitat for adult *L. concolor* in nearshore reaches. These streams therefore contain populations of adult *L. concolor* that are thriving and in high densities, but lower in total numbers than populations in upper reaches of larger streams.

Stochastic phenomena which occur in marine environments can lead to extremely high mortality rates for marine ichthyoplankton through mechanisms such as starvation,

predation, or advection away from suitable larval or adult habitats (Houde, 1989; Doherty, 1991). These events have strong effects on observed patterns in recruitment, and ultimately on adult population and community structure for species of fish with pelagic marine larval phases (Doherty & Fowler, 1994; Pfister, 1996). Organisms with amphidromous life cycles are similarly subject to high mortality rates that take place during their marine larval stage (McDowall, 1996; Radtke & Kinzie, 1996). The amphidromous fish communities in Hawaiian streams, therefore, are arguably structured to a large degree by events or environmental factors that occur beyond the boundaries of the streams themselves, and can therefore be thought of as open communities (McDowall, 1996).

Unlike their marine counterparts, amphidromous species have an additional life-history stage during which they may be subject to high mortality rates. The time period which begins at hatching and extends until the larvae pass out of the mouth of the stream into the ocean represents a critical step in the amphidromous life cycle, during which biological, hydrographic, geomorphometric, and anthropogenic stream features may affect migratory success and survival (Iguchi & Mizuno, 1990, 1999; Bell & Brown, 1995; Lindstrom, 1998; Moriyama et al., 1998; Way et al., 1998; March et al., 2003). Studies of seaward migrating amphidromous gobies in Japan and the Caribbean have indicated that larvae hatched in headwater stream reaches located a long distance from the ocean experience high rates of mortality during their seaward migration (Bell & Brown, 1995; Moriyama et al., 1998; Iguchi & Mizuno, 1999). In most cases, mortality in pre-marine goby larvae has been attributed to starvation. To date, there have been no studies in Hawai‘i that have focused on the migratory success of larval ‘o‘opu as they move downstream towards the ocean.

Because *L. concolor* is the only species of ‘o‘opu commonly abundant in the high elevation headwater reaches of large streams, it is arguably the species most likely to

experience significant losses of larvae during seaward migrations. The fact that adult *L. concolor* can also be found near the ocean in small streams with terminal waterfalls provided an opportunity to compare the numbers of larvae successfully entering the ocean from both stream types. This chapter describes a study that addressed the null hypothesis that there were no differences in the number of larval *L. concolor* entering the ocean from terminal-waterfall streams versus estuary streams. This null hypothesis is potentially valid from a biological perspective. Streams and rivers in Japan and Dominica where high mortality of drifting larval gobies has been observed (Moriyama et al., 1998; Bell & Brown, 1995) are generally much longer than most Hawaiian streams. The likelihood of larval gobies perishing prior to arrival in the ocean is, therefore, much higher in the longer streams and rivers located on these islands than in Hawaii's comparatively short streams. A prediction could be made, therefore, that even Hawaii's largest streams are still short enough that high mortality rates will not be observed for larval *L. concolor* migrating to the ocean. One of the alternative hypotheses addressed was that large estuary streams typically have more larval *L. concolor* successfully entering the ocean due to the fact that these streams have a greater total amount of their preferred Aa reach habitats in high elevation reaches and multiple inland tributaries and thus contain greater total numbers of spawning adult fish able to produce larvae at any given point of time. A second alternative hypothesis predicts that the opposite pattern would be observed: more larval *L. concolor* enter the ocean from small terminal-waterfall streams because, after hatching, the total linear distance to be traveled from hatching sites to the ocean is orders of magnitude shorter than they are for larvae hatched in the upper reaches of estuary streams.

## Study Sites

Samples of larval *L. concolor* were collected from four streams on the island of Hawai'i: Manowaiopae, Manoloa, Hakalau, and Umauma Streams (Figure 10). Manowaiopae and Manoloa Streams were selected because they are first-order streams with terminal waterfalls that have high densities of adult *L. concolor* located at low elevations and a short distance from the ocean. Hakalau and Umauma Streams are both third-order streams that have high densities of adult *L. concolor* in their headwater reaches and very low densities in the middle and terminal reaches. Sampling was conducted as near to the mouths of all four streams as possible. In Manowaiopae and Manoloa Streams (Sites 1 and 2), sampling stations were located at the top of the terminal waterfall. In addition to the two nearshore sites (Sites 4 and 7) in Hakalau and Umauma Streams, sampling was also conducted at three inland sites (sites 3, 5, and 6) located in high elevation reaches where adult *L. concolor* were resident in high densities (Figure 10).

## Methods

### Drift net sampling

Samples of larval *L. concolor* ( $n = 115$ ) were collected with stationary drift nets during the Spring seasons (February through April) of 2003-2006. Drift nets used in this study had square mouths that measured 31 X 31 cm with 200  $\mu$ m mesh. Nets were 1 m in overall length and had 1L collection bottles at the cod ends. Drift nets were secured in the thalweg by using rebar pounded into the substrate (Figure 11) and were left in place for up to 50 minutes per collecting period, or until they became clogged with suspended material.

Drift of larval amphidromous fishes has been shown to peak during a three-hour period following sunset (Iguchi & Mizuno, 1990; Lindstrom, 1998). A post-sunset peak in seaward drift was confirmed in *L. concolor* during an investigation of diel temporal patterns

Table 1. Sample site descriptions, with the number of drift samples collected at each site in parentheses

Site	Location	Elevation (m)	Distance from ocean(m)	Description
1	Manowaiopae (10)	73	95	Terminal Waterfall
2	Manoloa (6)	30	38	Terminal Waterfall
3	Upper Umauma (35)	366	4,848	Large - Inland
4	Lower Umauma (15)	30	718	Large - Nearshore
5	Upper Hakalau (18)	341	5,070	Large - Inland
6	Upper Hakalau (6)	360	5,290	Large - Inland
7	Lower Hakalau (24)	3	184	Large - Nearshore

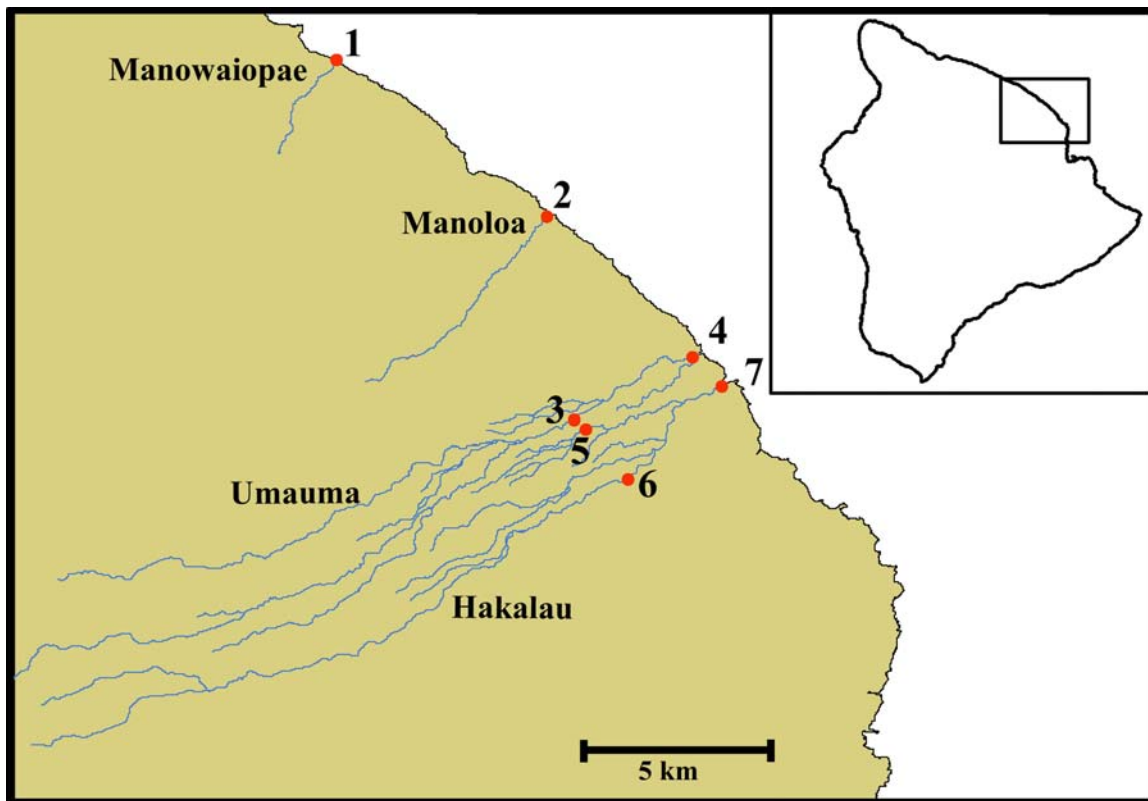


Figure 10. Location of sampling sites.



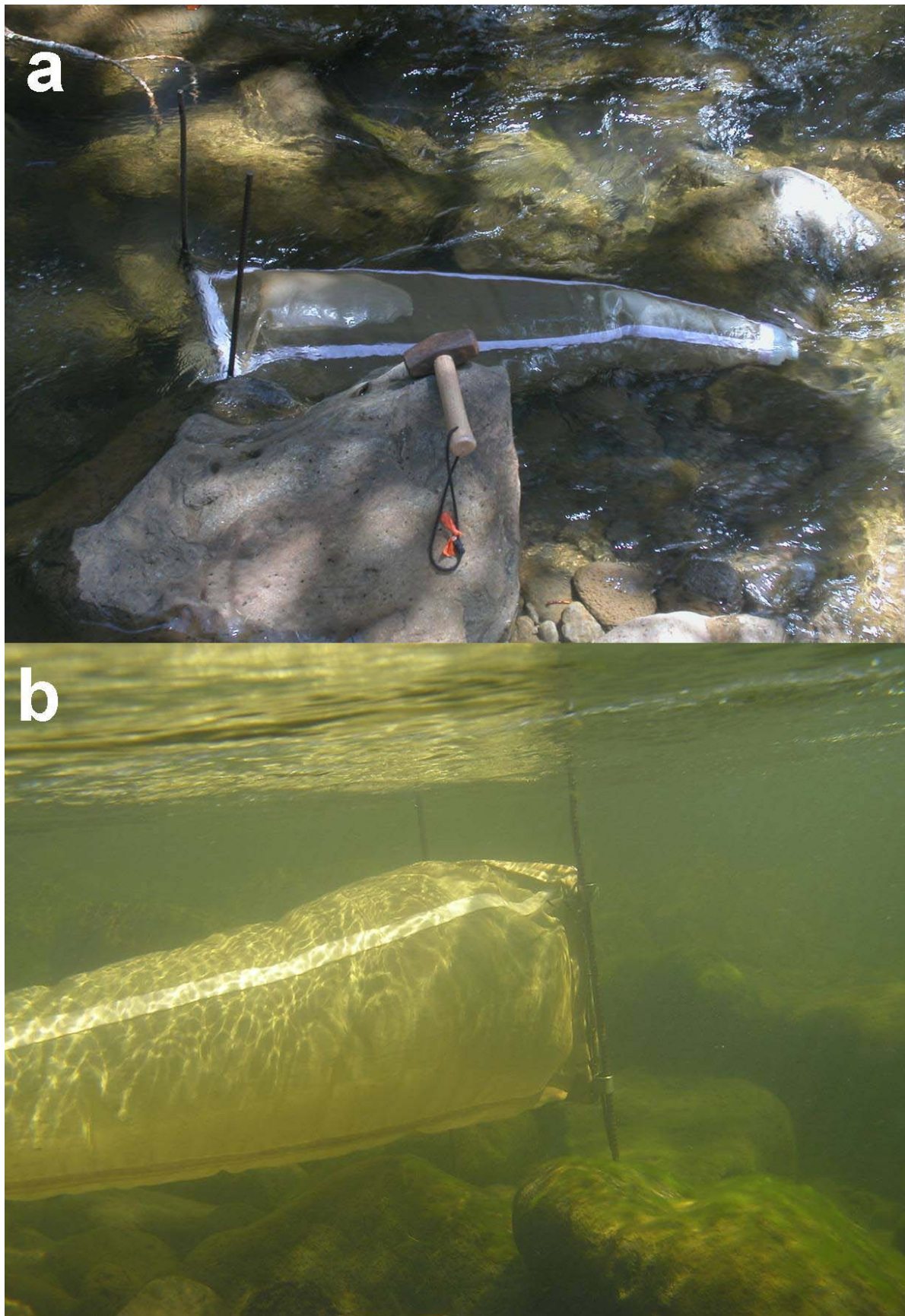


Figure 11. Drift nets employed. (a) view from above, (b) underwater view.

in their seaward migration (Chapter 3). Sampling effort was, therefore, concentrated during the first three hours following sunset. Sites were visited on a random schedule of sampling days throughout the Spring field seasons.

The large amounts of organic material and debris in each sample initially made sorting of samples in the laboratory extremely inefficient and difficult, and resulted in a backlog of unsorted samples. When the larvae of amphidromous gobies are preserved and held in formalin for extended periods, color characteristics critical for species identification are lost (Lindstrom, 1998; Bell, 2006 in press; D. Kuamo'o, pers. comm.). Early difficulties with sample sorting indicated a need for a procedure to separate larvae from the associated suspended material in each sample. A protocol was devised from the suggestion by Lindstrom (1998) that took advantage of the swimming behavior of larvae to separate them from suspended material collected simultaneously in drift nets. Newly hatched amphidromous gobies in Hawai'i, and elsewhere, exhibit a vertical swimming behavior: larvae execute an extended burst of vertical swimming up into the water column, followed by a short period of head-first sinking (Ego, 1956; Todd, 1975; Iguchi & Mizuno, 1990; Lindstrom, 1998). This behavior maintains the position of larvae high in the water column, minimizes contact with bottom substrate, and facilitates their movement downstream. At the end of each sampling period, the material collected in the drift net was rinsed out of the cod end into a clear plastic pitcher, and suspended material was allowed to settle to the bottom (Figure 12). Larval *L. concolor* that swam upward were then decanted into a 50 mL plastic container and fixed with 5% formalin. By using this technique, a large number of samples could be sorted and the larvae contained in each counted and identified in a relatively small amount of time. The species of the larvae collected in drift nets was determined by using the dichotomous identification key to larval 'o'opu constructed by Lindstrom (1998).





Figure 12. Example of the procedure used to separate larvae from associated material in each sample. (a) receptacle after sample from drift net was first emptied into the pitcher. (b) 15 minutes later, debris has settled to the bottom and *L. concolor* larvae have swum towards the surface at which point they were poured into a sample bottle.

## Surveys of adult *L. concolor*

Underwater visual surveys were conducted in 1-km reaches upstream of each sampling site to determine the population densities (number/m<sup>2</sup>) of potentially spawning adult *L. concolor*. Within each survey reach, adult *L. concolor* were counted in randomly located quadrats that were up to 3 meters in length and width (Baker & Foster, 1992). Density data collected during underwater surveys were combined with data collected by Hawai'i Division of Aquatic Resources personnel between the years of 1989 and 2003.

## Data Analysis

Larval density was calculated for each sample by using an equation described by Saltveit et al. (2001):

$$N_t = \frac{n \cdot 60}{\left( \frac{v_1 + v_2}{2} \right) A t} \cdot 100$$

Where  $N_t$  = number of larvae collected per 100 m<sup>3</sup> water filtered,  $n$  = total number of larvae collected,  $v_1$  = water velocity (m/s) measured at the mouth of the drift net at the beginning of the sampling period,  $v_2$  = water velocity at the end of the sampling period,  $A$  = cross sectional area of the drift net (m<sup>2</sup>) and  $t$  = sampling time (s).

Drift densities were adjusted in an attempt to account for differences in the cross-sectional areas of the streams at each sampling site as follows: The value of  $A$  in the above equation was decreased for samples collected at sites 2-7 on an order of magnitude equal to the proportional difference in the cross sectional area of the stream channel at each site compared to the cross sectional area of Manowaiopae Stream at Site 1 (the smallest of the four streams). For example, if the cross sectional area of Manowaiopae Stream at Site 1 was 30% smaller than the cross sectional area of lower Hakalau Stream at Site 7, the value of  $A$

for Hakalau samples was multiplied by .30. The larval density ( $N_i$ ) calculated for a sample collected at site 7 on Hakalau Stream was thereby mathematically inflated and, as a result, roughly corresponded to that for a sample collected with a drift net that had an opening proportional to the larger stream cross section (Figure 13).

In an attempt to stabilize variances and normalize distributions, data were transformed prior to analysis by adding 1 to each larval density value and then taking the natural log (Sokal & Rolf, 1995). Mean larval densities at the seven sites were compared by using Kruskal-Wallis One-Way Analysis of Variance (ANOVA), as was the pooled data from each reach type (Large-Headwater, Large-Nearshore, or Terminal Waterfall). Data collected at inland and nearshore reaches of a single stream do not represent independent samples, and thus do not meet one of the assumptions associated with Analyses of Variance. Larval drift densities collected at inland and nearshore sites in the same watershed were, therefore, compared by using Wilcoxon Signed Rank Sum test (a non-parametric paired t-test). Drift densities from samples collected during the same week at the inland and nearshore sites in Hakalau and Umauma Streams were plotted to gain a more detailed understanding of drift patterns within each watershed.

## **Results and Discussion**

Highly significant differences were observed in the mean drift densities collected at the seven sampling sites ( $p < 0.0001$ ; Figure 14). The highest larval densities were collected at Site 1, located at the top of the terminal waterfall in Manowaiopae Stream. Manowaiopae Stream had high densities of adult *L. concolor* (Table 2) in a relatively short nearshore reach that begins at the top of the terminal waterfall and extends upstream for less than 1 km. The lowest mean larval densities were collected at sites 4 and 7, located in nearshore reaches of Umauma and Hakalau Streams, respectively. Both Umauma and Hakalau Streams had high

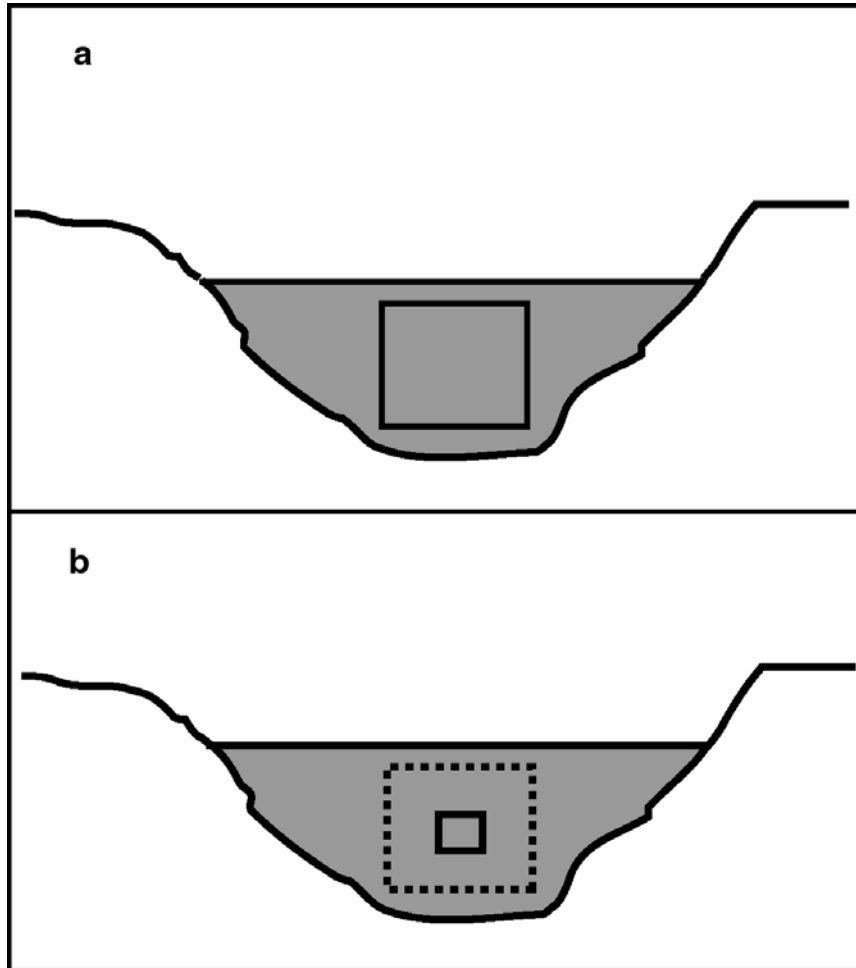


Figure 13. Diagram representing the mathematical adjustment of larval density values: (a) stylized cross-section of Manowaiopae Stream at site 1, with the solid square representing the area occupied by the drift net opening; (b) the same sized net in the larger Hakalau Stream channel at site 7. The dashed line represents the proportion of the stream channel covered by the mathematically adjusted net opening.

densities of adult *L. concolor* in high elevation reaches (near sites 3, 5, and 6; Table 2), but low densities in lowland reaches (near sampling sites 4 and 7). Within Umauma Stream, higher densities of *L. concolor* larvae were collected at the inland site (Site 3) than at the nearshore site (Site 4; Figure 14). A similar pattern existed in Hakalau Stream, with higher densities of larvae collected at sites 5 and 6, located approximately 5 km inland from the stream mouth, than at the nearshore Site 7.

Table 2. Densities of adult and larval *L. concolor* observed at each study site.

Site	Location	Adult Density (N)	Larval density (mean±s.e.)
1	Manowaiopae	2.86 (30)	1165 ± 487.26
2	Manoloa	1.84 (181)	128 ± 83.07
3	Upper Umauma	0.83 (42)	776 ± 273.52
4	Lower Umauma	0.21 (27)	1232 ± 1227.86
5	Upper Hakalau	1.01 (51)	966 ± 56.15
6	Upper Hakalau	3.42 (30)	405 ± 156.21
7	Lower Hakalau	0 (184)	48 ± 29.08

When larval density data from the three reach types (Terminal Waterfall, Large-Inland, and Large-Nearshore) were combined, a clear pattern emerged, with significantly more larval *L. concolor* entering the ocean from the small streams with terminal waterfalls than from the larger streams with terminal estuaries (Figure 15). High numbers of *L. concolor* larvae were collected in the larger streams, but almost exclusively at high elevation sites located in reaches with high densities of *L. concolor* adults.

The null hypothesis that there were no differences between terminal-waterfall streams and estuary streams in the number of *L. concolor* larvae entering the ocean was, therefore, rejected. These results support the alternative hypothesis that more larval *L. concolor* successfully entered their marine habitats from small streams with terminal waterfalls. The low numbers of larvae collected in the nearshore reaches of Umauma and Hakalau Streams could be considered somewhat surprising, since larval *L. concolor* were so prevalent in drift

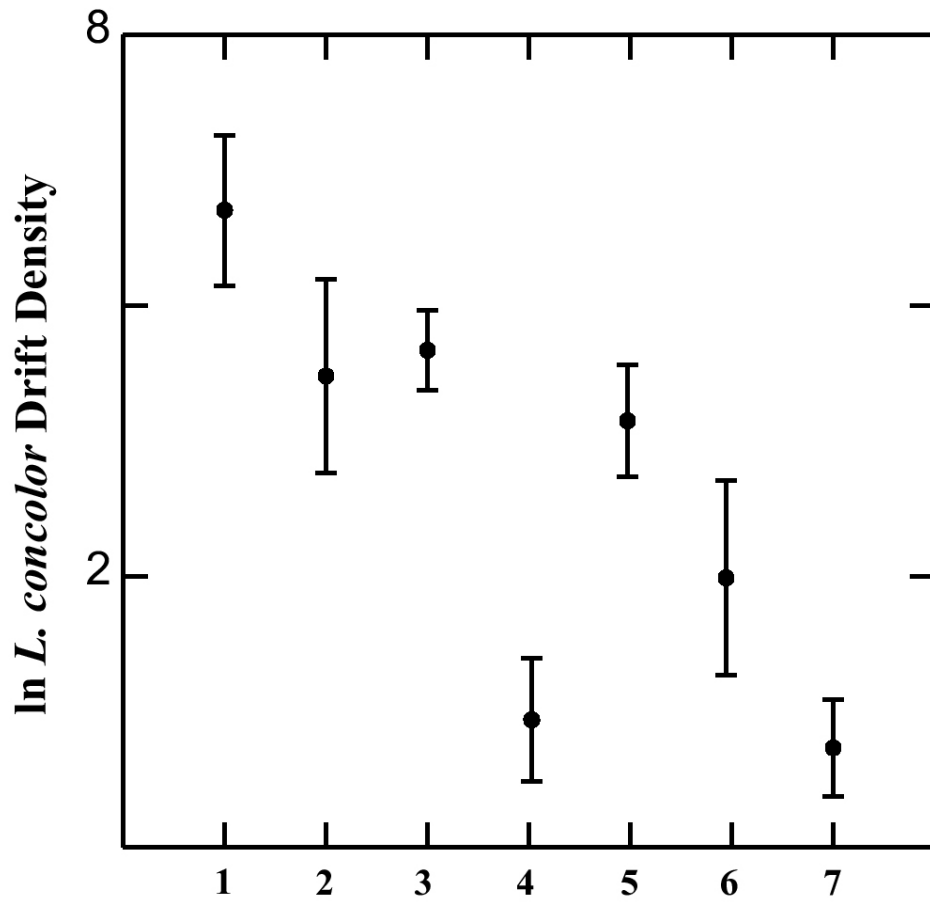


Figure 14. Means and standard error of the  $\ln(x+1)$  transformed larval densities collected at the seven sample sites.



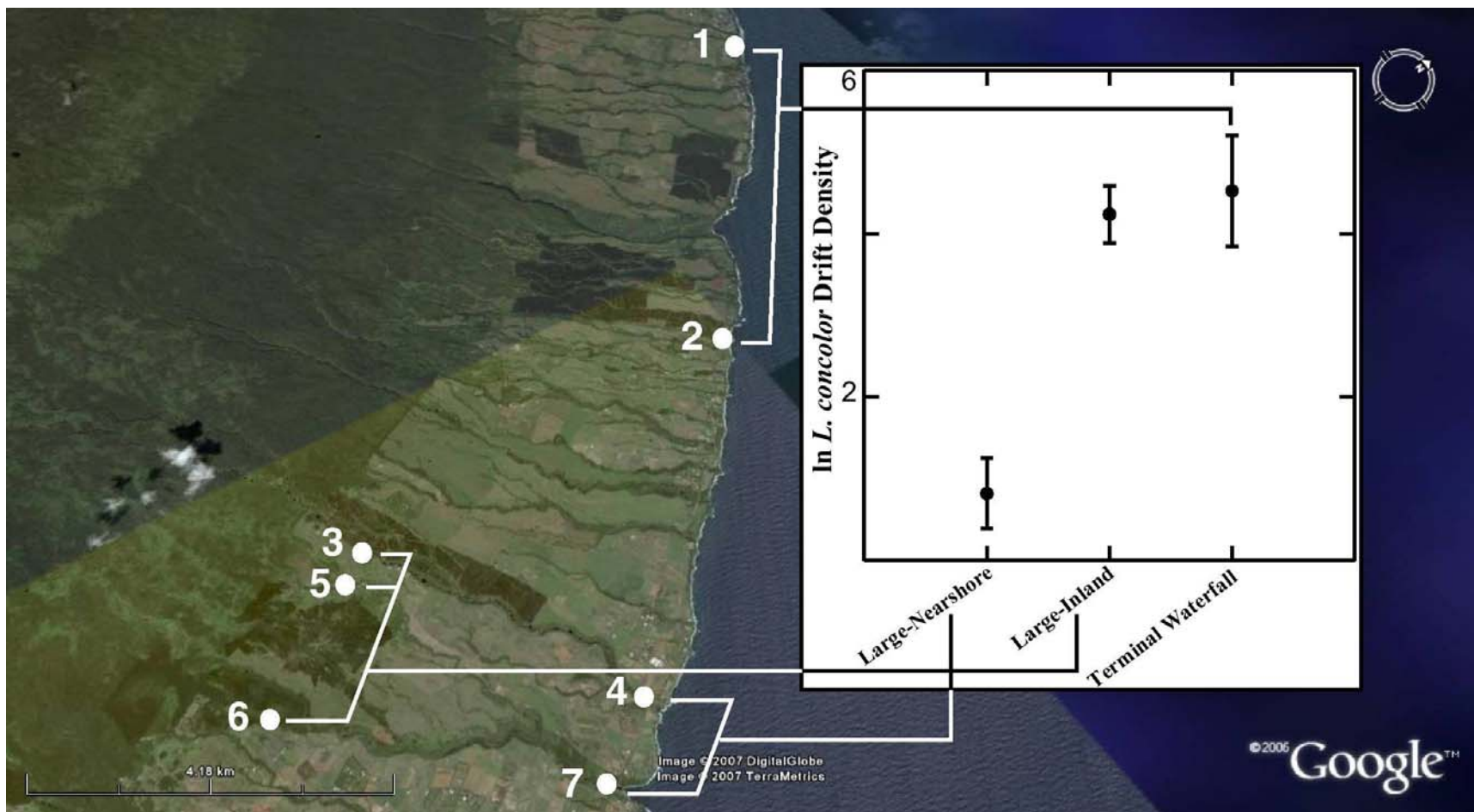


Figure 15. Means and standard errors of larval densities collected in each reach type.

samples collected in the upper reaches of those streams. The results of the paired t-test performed on samples collected at inland and nearshore sites in Umauma and Hakalau Streams confirmed that the larval densities collected at inland sampling sites were significantly higher than at nearshore sites ( $p < .0001$ ; Figure 16). One potential interpretation of this observed pattern is that of the many larvae that hatched at inland sites, a small subset of them survived the journey downstream to be collected at the nearshore sites, and therefore a number of them successfully completed their seaward migration.

A week-by-week plot of the paired sample data collected in the two estuary streams indicated that an alternate interpretation may be more appropriate. During most weeks when large numbers of larval *L. concolor* were collected at inland sites, none were collected at the nearshore sites (Figures 17 & 18). There were two general exceptions to this pattern: 1) during Week 12 in Umauma Stream, the opposite pattern was observed, with a high number of larval *L. concolor* collected at the nearshore site, and none collected at the inland site, and 2) during weeks 4, 13, and 23 in Hakalau Stream, and Week 3 in Umauma Stream, large numbers of larvae were collected at *both* inland and nearshore sites.

The most commonly observed pattern of large numbers of newly hatched *L. concolor* occurring at inland reaches of large streams but none in the nearshore reaches during the same week suggests that larvae hatched in upper reaches did not successfully complete their seaward migrations. *Lentipes concolor* larvae emerge from demersally spawned eggs in a highly under-developed state, lacking functional digestive tracts, and are therefore unable to feed until they arrive at their oceanic feeding sites (Lindstrom, 1998; Bell & Brown, 1995). An oil droplet functions as a yolk-sac and provides nutrition

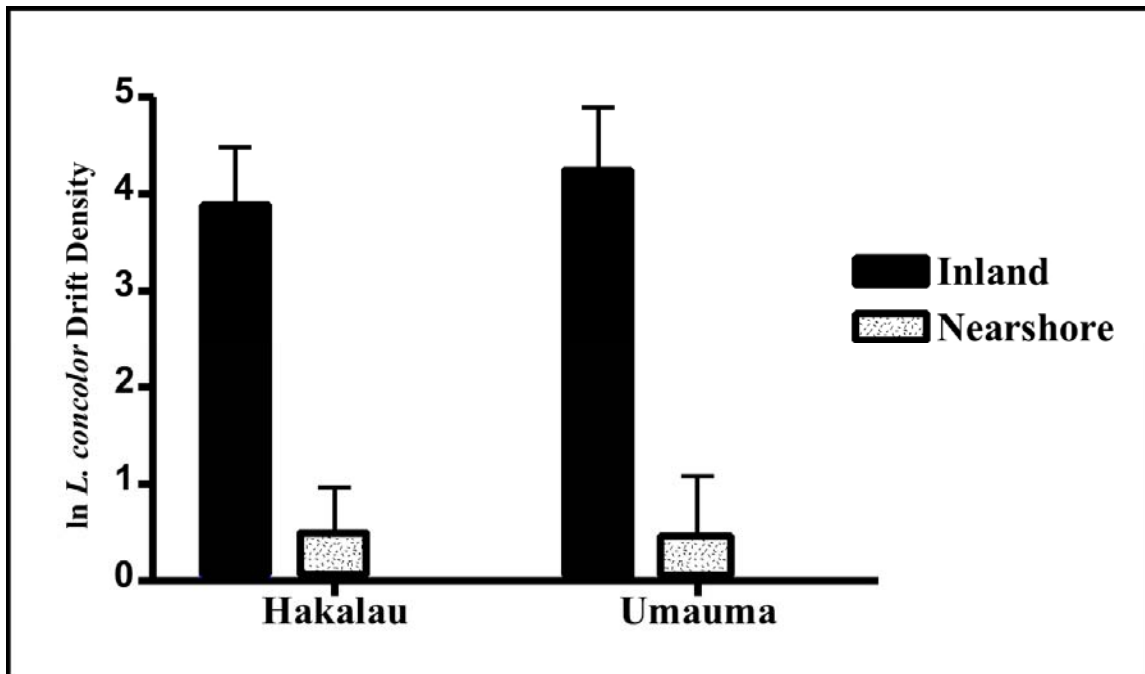


Figure 16. Comparison of paired samples collected at inland and nearshore sample sites in the two estuary streams.

to the larvae for a short period. High mortality rates of larvae during the downstream journey towards the ocean have been observed in other amphidromous fishes and have usually been attributed to starvation. Bell & Brown (1995) estimated that mortality rates for newly hatched *Sicydium punctatum* were as high as 50% hour<sup>-1</sup> in streams on the island of Dominica in the West Indies. Moriyama et al. (1998) concluded that in normal or low river flow conditions in Japan, most *Rhinogobius brunneus* larvae hatched in high gradient upstream reaches starved to death before reaching the sea. The larvae of several species of amphidromous fishes, including *L. concolor*, have been observed to die after a short time if held in pure fresh water. Larval *Awaous guamensis* (Ego, 1956) and the Caribbean species *Sicydium punctatum* (Bell & Brown, 1995) died after being held in fresh water for only four days. Tomihama (1972) reported that larvae of the Hawaiian endemic *S. stimpsoni* died after five days in fresh water. Larval *L. concolor* hatched in captivity rapidly depleted their maternally provided energy sources and died in less than 36 hours if not provided with exogenous nutritive sources (Lindstrom, 1998). The larvae of the Japanese stream goby, *R. brunneus*, lived for seven days in fresh water (Iguchi & Mizuno, 1999), but were observed to reach an irrecoverable starvation state (ISS) after approximately six days. If it is assumed that *L. concolor* larvae similarly reach an ISS at some point before death in fresh water, it is clear that the larvae of this species have a brief “window of opportunity” to complete their seaward migrations (Lindstrom, 1998).

Stream features that exist between hatching sites and the ocean can potentially increase the amount of time that pre-marine *L. concolor* larvae spend in-transit on their way to oceanic feeding sites and consequently can decrease their chances for survival. Low water velocity habitats in midreach, terminal reach, and terminal estuaries can retain the passively migrating larvae in freshwater habitats which increases the likelihood of

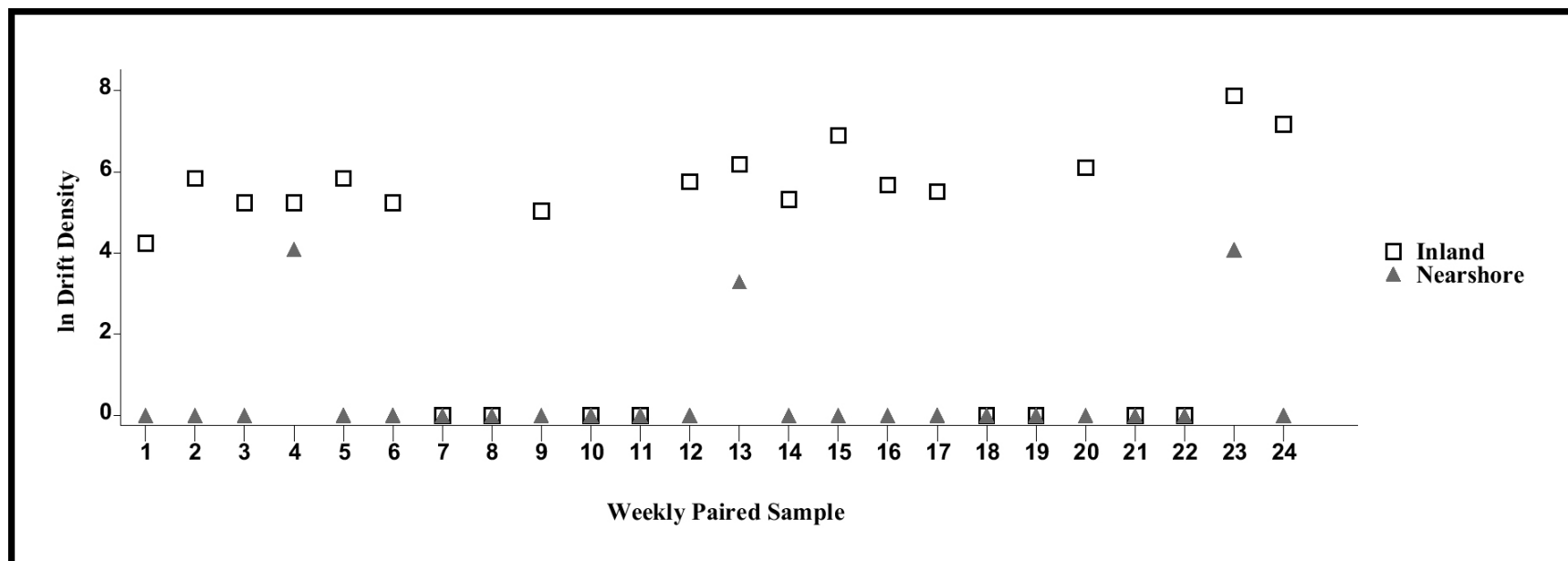


Figure 17. Weekly comparison of paired samples collected at the inland and nearshore sites in Hakalau Stream.

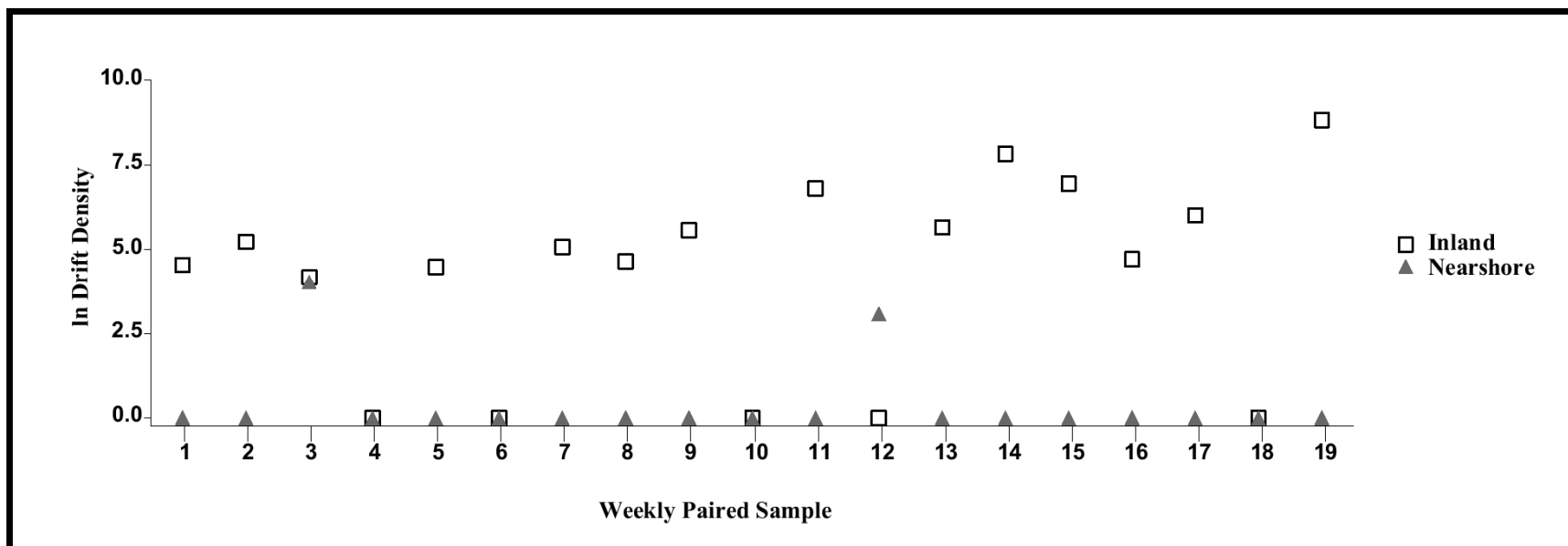


Figure 18. Weekly comparison of paired samples collected at the inland and nearshore sites in Umauma Stream.

starvation. Terminal reaches and estuaries also often have high densities of introduced freshwater and itinerant marine zooplanktivorous fishes (McRae, 2001) that could prey upon drifting larvae.

Low water velocity habitats, such as plunge pools, side pools, and backwater eddies, are abundant in the Aa and Aa-Bb reaches that are common in the headwaters and upper midreaches of Hawaiian streams. On the geologically younger islands of the Hawaiian Archipelago (e.g., Hawai‘i and Maui), waterfalls are abundant throughout the midreaches of perennial streams (Figure 19). Their associated plunge pools can be very deep and wide even during periods of low discharge in these watersheds. Each of these plunge pools, during all but the most intense freshets, represents a naturally semi-impounded habitat, inside which water velocities can be practically imperceptible. These midreach low-water-velocity habitats are likely significant obstacles to larval *L. concolor* as they migrate to sea. Plunge-pools can also contain large populations of introduced poeciliid fishes (e.g., guppies, *Poecilia reticulata* and swordtails, *Xiphophorus helleri*) that may prey upon larvae that are entrained in these low-water-velocity habitats.

Similarly, long, sinuous estuaries not only increase the amount of time that pre-marine larvae spend in transit to the ocean, but they also are often home to large populations of native and introduced zooplanktivorous freshwater and marine fishes (McRae, 2001). The endemic āholehole, *Kuhlia xenura*, feed actively on food items drifting downstream and are common in terminal stream reaches throughout Hawai‘i. Introduced mosquitofish, *Gambusia affinis*, are well known larvivores and zooplanktivores (Arthington, 1991; Komak & Crossland, 2000) that likely feed on larval gobies that end up in the slack-water habitats they prefer (McRae, 2001). Shortfin mollies, *Poecilia mexicana*, swordtails, *Xiphophorus helleri*, and tilapia, *Oreochromis*



Figure 19. Reach in Umauma Stream measuring approximately 750 m; located immediately downstream of site 3.



*mossambicus* are common introduced fishes in Hawaii's terminal streams and estuaries (Devick, 1991; McRae, 2001) that are known to be at least opportunistically zooplanktivorous.

In spite of the fact that larvae were infrequently collected in nearshore reaches of the larger streams sampled in this study, this does not necessarily suggest that larvae hatched in the upper reaches of these streams never successfully attain the ocean. Drift net sampling could be safely and effectively performed only during low to slightly elevated flow conditions, and the results presented here therefore apply only to periods when these conditions existed. Larvae that hatch in upper reaches could be transported to the ocean very rapidly during one of the freshets that occur so frequently in Hawaiian streams and this possibility should be addressed in future research.

Like many species of marine and stream gobies, *L. concolor* are highly fecund, with clutch sizes as high as 24,900 eggs (Kinzie, 1993). The rare occurrence of high numbers of *L. concolor* larvae in nearshore reaches of large streams (see Figures 14 and 15) during periods when stream flow was low enough to drift sample could have been the result of spawnings performed by the small number of adults located relatively near sample sites 4 and 7 (Table 2). These results suggest that although lower midreaches of larger streams may contain only low numbers of adult *L. concolor*, these individuals may be contributing the majority of successfully migrating larvae in these watersheds, and should therefore be a conservation priority

The high demand for fresh water to be used in coastal developments and large-scale agriculture in Hawai'i has resulted in extreme alterations of stream habitats through mechanisms such as channelization and water diversions. Anthropogenic destruction of stream habitats commonly occur in the lower reaches of Hawaiian streams and result in

the elimination of suitable habitats for adult gobies. The removal of water to be used in coastal development projects or for the irrigation of sugar cane has resulted in extreme alterations of the natural flow regime in many Hawaiian streams. The results presented in this chapter suggest that these types of human perturbations may be especially threatening to the endemic *L. concolor*. Channelization that leads to the destruction of suitable habitat for adult *L. concolor* in the lower reaches of larger streams eliminates the most successfully reproducing individuals from that watershed. Altered stream channels also provide high-quality habitats for large populations of invasive fishes that could potentially prey upon larvae migrating from upper reaches. The diversion of stream water results in artificially reduced discharge and lower water velocities. This, in turn, lengthens the amount of time larval *L. concolor* hatched in mountainous reaches must spend in transit to the ocean and increases the threat of starvation.

The results of the work presented here suggest that the highest quality habitats for adult *L. concolor* primarily lie in nearshore stream reaches. Because of this, conservation efforts for this endemic species should focus on the protection and restoration of areas that could potentially support thriving populations of adult *L. concolor* in stream reaches close to the ocean. Priority should be given to the protection of terminal-waterfall streams that have large populations of adult *L. concolor*. In large estuary streams, emphasis should be placed on the need to identify and restore habitats that lie at the downstream end of the longitudinal distributions of adult *L. concolor*. The restoration of natural flow regimes to streams that have been heavily diverted will also increase the chances that larvae produced in large streams will successfully reach the ocean and proceed with the completion of their complex life cycles.

## **CHAPTER 3**

### **TEMPORAL PERIODICITY IN THE SEAWARD MIGRATION OF LARVAL *LENTIPES CONCOLOR***

## Introduction

Amphidromous species are often large components of the fish communities that inhabit streams on oceanic islands. In the Hawaiian Islands, the entire assemblage of native stream-dwelling fishes is amphidromous. These closely related species (all in the suborder Gobioidae) are, therefore, potentially subject to the ecological constraints and selective pressures associated with both freshwater and marine environments. Because larvae must successfully move downstream from hatching sites to the ocean, it is at this point in their lives when they are subject to the widest range of freshwater and marine factors that could impact their survival. To date, very little is known about the ecological characteristics of the earliest life history stages of Hawaiian amphidromous fishes. The goal of the study described in this chapter was to document temporal patterns in the downstream migration, or drift, of larval *Lentipes concolor* at the 24-hour (or diel) and lunar time scales.

Variability in the occurrence of reproductive events, such as spawning and hatching, have been shown to be closely linked to temporal cycles at different scales for both freshwater and marine fishes (Muth & Schmulbach, 1984; Taylor, 1984; Carter et al., 1986; Robertson et al., 1988; Robinson et al., 1998; Copp et al., 2002; Zitek et al., 2004). Hypotheses regarding the adaptive advantages of distinct temporal periodicity in spawning have included increased dispersal ability of larvae due to favorable tidal conditions, the avoidance of consumption of larvae by visual predators, and the synchronization of the arrival of larvae at marine feeding sites with the presence of planktonic food sources (Robertson et al., 1990).

Distinct periodicity in the downstream drift of larval amphidromous gobies has been observed primarily at the diel time scale. In Japan, *Rhinogobius brunneus* exhibited

a reach-dependent diel drift pattern (DDP) (Iguchi & Mizuno, 1990). In low-gradient coastal stream reaches, sharp peaks in the numbers of larval *R. brunneus* drifting downstream occurred after sunset. In high-gradient stream reaches, however, no distinct DDP was observed for this species; larvae moved towards the sea at all hours of the day and night. Moriyama et al. (1998) hypothesized that the lack of distinct post-sunset peaks in the DDP of larval *R. brunneus* in steep mountainous reaches was due to the fact that, although larvae were hatching after sunset, they soon became entrained in areas of turbulent flow (i.e., side pools, eddies, and backwater areas) that are abundant in high-gradient stream reaches. Larvae trapped in turbulent areas escaped entrainment and moved downstream at random times during the day.

Other investigations of temporal drift patterns in amphidromous gobies have focused primarily on low-gradient reaches near the mouths of estuary streams. Bell (2006 in press) reported that larval drift of *Sicydium punctatum* in a large stream on the island of Dominica, West Indies, was primarily nocturnal. In the coastal reach of Wainiha Stream (a large estuary stream) on the island of Kauaʻi, the drift of unidentified goby larvae was also nocturnal, and was restricted to the first three hours following sunset (Lindstrom, 1998). The larvae of many species of primary freshwater fishes in rivers on large continents also show distinct diel patterns in downstream drift with peaks typically occurring at night (Muth & Schmulbach, 1984; Carter et al., 1986; Robinson et al., 1998; Copp et al., 2002; Zitek et al., 2004). It is generally assumed that the larvae of species that inhabit lotic habitats drift at night as an adaptive strategy to avoid the abundant visually-oriented predators that typically feed on drifting prey items (Allen, 1995).

Larval *L. concolor* hatch in high-gradient stream reaches with complex flow characteristics that could entrain larvae. It was therefore predicted that no distinct diel drift pattern would be observed. An alternative prediction made *a priori* was that the diel drift pattern of larval *L. concolor* would peak during the hours following sunset due to the selective pressure exerted on the timing of hatching by visually-oriented predators inhabiting lower stream reaches and marine environments.

Although distinct lunar periodicity in the numbers of larval amphidromous gobies drifting downstream has not been observed during drift sampling (Lindstrom, 1998; Bell, 2006 in press), it has been widely observed in the timing of spawning for many species of benthic-brooding marine species that have pelagic larvae (Robertson et al., 1990). Because many of the reproductive characteristics of amphidromous gobies more closely resemble those of their marine counterparts than they do those of primary freshwater fishes (Kinzie, 1993), it was predicted that lunar periodicity would be observed in the occurrence of larval *L. concolor* moving downstream.

## **Methods**

### **Diel Drift Patterns**

To identify diel patterns in downstream drift of pre-marine *L. concolor*, 24-hour drift net sampling was employed on 11 separate dates during the Spring seasons of 2003-2006. Sampling took place near the mouths of Manowaiopae and Manoloa Streams (Sites 1 and 2) as well as in the upper reaches of Hakalau and Umauma Streams (Sites 3 and 5; Figure 9). Drift nets were left in place for up to 50 minutes and were emptied once every hour. The velocity of the water flowing into the nets was measured at the start and end of each hourly set. On dates when streams carried high amounts of suspended debris, drift nets were monitored closely and removed once they became clogged. Larvae were

separated from the associated suspended material in each sample by decanting them after they swam towards the surface as debris settled to the bottom (see Chapter 2 – Methods). Five-percent buffered formalin was used to fix and preserve larvae until samples could be sorted under a dissection microscope. The density of larvae (number · 100m<sup>-3</sup> of water filtered) captured during each hour was calculated by using the equation described by Saltveit et al. (2001) (see Chapter 2 - Methods).

Min/max autocorrelation factor analysis (MAFA) was performed to identify common trends in the 24-hour sample data. MAFA (Solow, 1994) is a type of principal component analysis (PCA) in which individual axes represent the amount of autocorrelation and association between variable  $Y_t$  and  $Y_{t+k}$ , where  $k$  is a time-lag ( $k = 1, 2, \dots$ ). In PCA, the first axis explains the majority of the variance in the data. In MAFA, the first MAFA axis has the highest autocorrelation with lag 1, and, as trends are associated with high autocorrelation, represents the main temporal trend in the data (Erzini, 2005).  $P$ -values obtained by a randomization process were used to determine how many of the 24-hour trends indicated by MAFA axes were significant. Canonical correlations were used as a measure of the relationships between individual sampling efforts and MAFA axes. To make the interpretation of factor loadings and common trends easier, larval density data from the 24-hour time series were standardized by subtracting the overall mean density from the larval density of each hourly sample and dividing by the standard deviation. All factor loadings and common trends produced by the MAFA are, therefore, unitless. The statistical software package Brodgar (<http://www.Brodgar.com>) was used to perform the time series analysis.



## Lunar periodicity

Drift net samples collected during the first three post-sunset hours on randomly selected dates during the spring seasons of 2003-2006 were analyzed by using periodic regression analysis. In order to perform the periodic regression, each sampling date was assigned a value which will herein be referred to as “lunar day”. The lunar day represented the number of days since the preceeding new moon, and ranged in value from 0 (for samples collected on dates that fell on a new moon) to 30 (samples collected immediately before a new moon). Each lunar day was then transformed into degrees by multiplying by  $2\pi$  radians to give each day an angular equivalent,  $\theta$ . The angular lunar day values were then incorporated as the independent variable in a simple linear regression model:

$$\text{larval density} = b_0 + b_1 \cdot \sin\theta + b_2 \cdot \cos\theta$$

where  $b_0$  is the mean larval density, and  $b_1$  and  $b_2$  are model coefficients which together define the range of oscillation of larval density and the point on the circular lunar scale at which larval density is at the maximum (deBruyn & Meeuwig, 2001; Bell, 2006 in press). In an attempt to stabilize variances and normalize distributions, drift data were transformed prior to analysis by adding 1 to each larval density value and then taking the natural log (Sokal & Rolf, 1995).

Analyses incorporated data collected in reaches that contained high densities of adult *L. concolor* (sites 1, 2, 3, 5, and 6). Periodic regression analyses were performed on the combined data from all five sites, as well as on data stratified by reach type: separate models were fitted to data collected at the mouths of both terminal-waterfall streams (combined data from sites 1 and 2) and in the upper reaches of the two estuary streams (sites 3, 5, and 6).

## Results and Discussion

### Diel periodicity

Larval *L. concolor* were collected during seven of the eleven 24-hour sampling efforts conducted during the 2003-2006 field seasons (Table 3). A high degree of

Table 3. Dates and locations of 24-hour sampling efforts.

Date	Location	Sampling site	Larvae collected? (Yes/No)	Abbreviation
20 February 2003	Manowaiopae	1	Yes	Manowai 1
26 February 2003	Manowaiopae	1	Yes	Manowai 2
16 April 2003	Manowaiopae	1	Yes	Manowai 3
22 April 2003	Manoloa	2	Yes	Manoloa 1
3 May 2003	Manoloa	2	Yes	Manoloa 2
13 February 2004	Lower Hakalau	7	No	----
17 February 2004	Upper Umauma	3	Yes	Umauma 1
26 February 2004	Lower Hakalau	7	No	----
28 March 2004	Upper Umauma	3	No	----
1 February 2005	Lower Hakalau	7	No	----
10 January 2006	Upper Umauma	3	Yes	Umauma 2

variability was observed in these 7 time series, with larvae present in samples collected during both daylight and nighttime hours (Figure 20).

The Min/Max Autocorrelation Factor Analysis produced 2 axes that illustrated common trends in the drift data (Figure 21). Axis 1 had a moderately high autocorrelation (0.748), and was statistically significant ( $p = 0.05$ ). The scores for the first MAFA axis (Figure 21a) were highest during the hours immediately surrounding sunset. The canonical correlations illustrating the relationships between 24-hour sampling efforts and the first MAFA axis indicated positive correlations for five of the seven time series: Manowai 2 and 3, Manoloa 1 and 2, and Umauma 1 (Figures 21b and c).

The significant temporal trend in larval drift of *L. concolor* represented by MAFA axis 1 suggests that downstream migration for this species most commonly takes place at

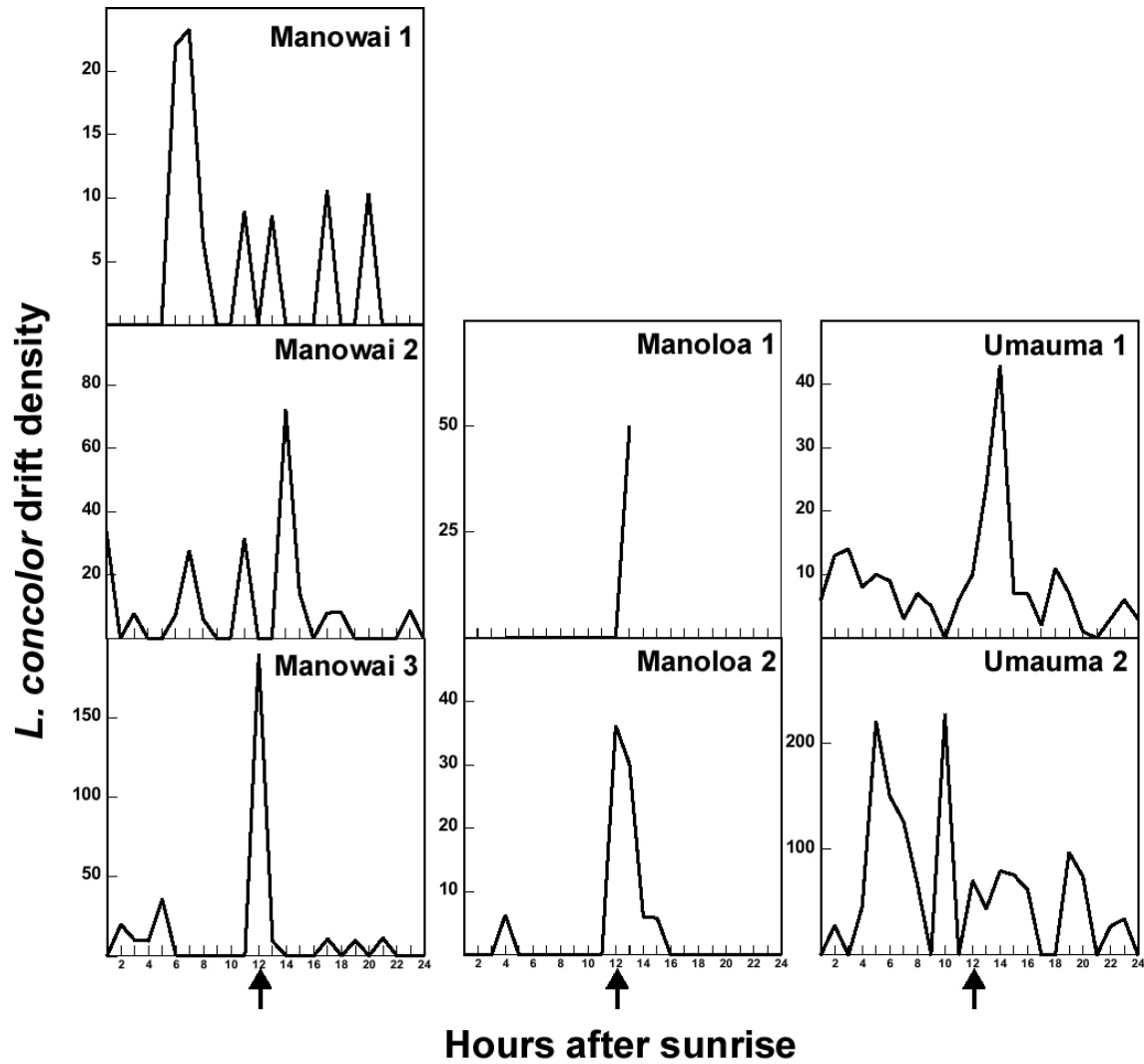


Figure 20. Daily drift patterns of larval *L. concolor* observed on seven separate dates at three sites (see Table 3). The position of black arrows on the x-axis indicates sunset.

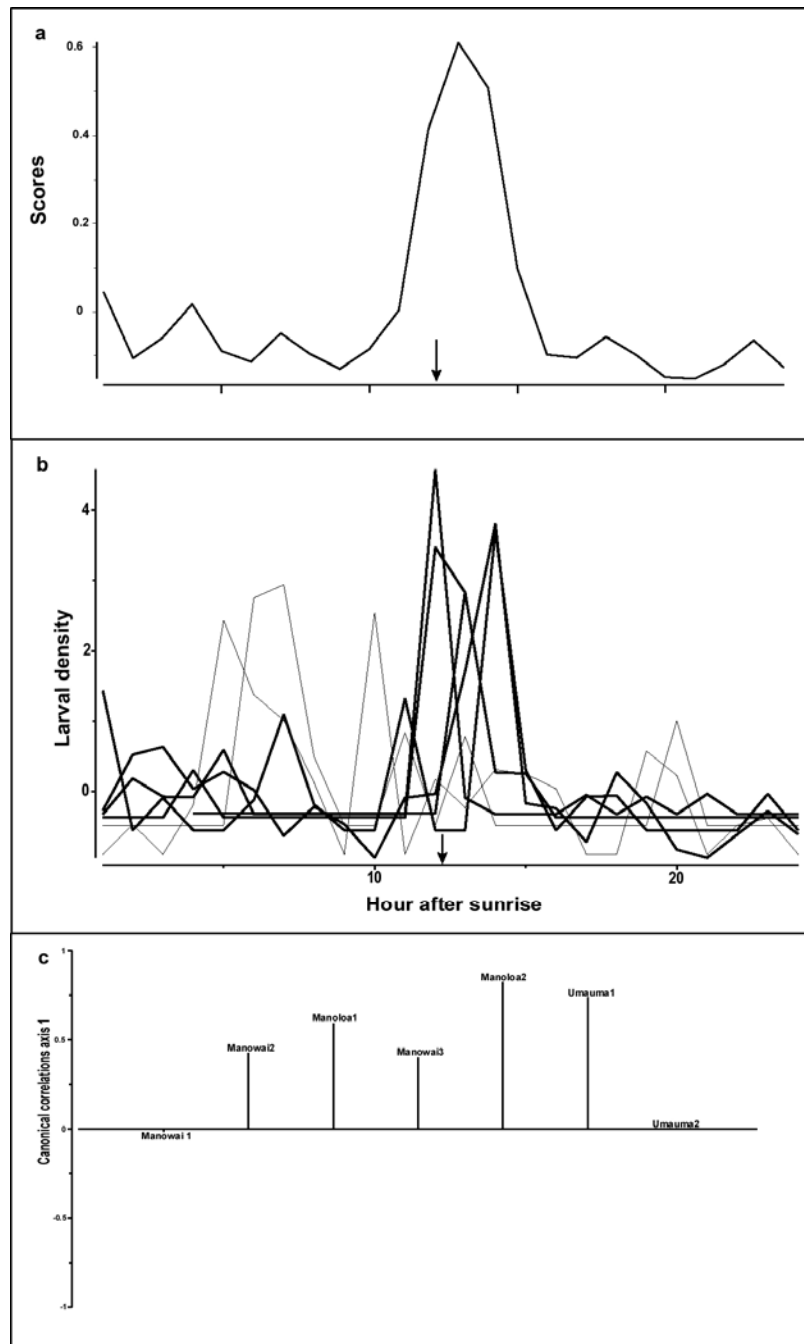


Figure 21. (a) MAFA axis 1, (b) the five 24-hour time series described by the common trend represented in MAFA axis 1, and (c) canonical correlations associated with each univariate time series with high loadings on MAFA axis 1. Position of black arrows on x-axis indicates sunset.

shortly after dusk (Lindstrom, 1998). The results presented here suggest that sunset-associated hatching commonly takes place in nests located in streams as well. A nocturnal drift pattern was also observed for larval *S. punctatum* in streams on the island of Dominica in the West Indies (Bell, 2006 in press). Larvae of the Japanese species *R. brunneus* were shown to be negatively phototactic and were stimulated to swim towards the surface in low-light conditions (Iguchi & Mizuno, 1999). It is likely that the drop in ambient light levels that occurs after sunset stimulates hatching of larval *L. concolor* from nests, and may similarly stimulate them to swim towards the surface which would accelerate seaward movement. The nocturnal downstream movement of larvae may have an adaptive advantage for avoiding the visually-oriented predators that inhabit terminal stream reaches and nearshore marine habitats.

The second MAFA axis had an autocorrelation of 0.598 and was not statistically significant ( $p = 0.106$ ). Canonical correlations indicated *negative* correlations between MAFA axis 2 and the 24-hour samples Manowai 1 and Umauma 2 (Figure 22c). Because the canonical correlations are negative, the lowest scores on the axis represent peaks in larval drift that occurred during daylight hours (Figure 22 a and b).

The prevalence of larval *L. concolor* in drift net samples collected during daylight hours could be related to the turbulence of the Aa stream reaches where sampling occurred. The timing of downstream drift in larval *R. brunneus* in Japan was dependent upon the type of reach that was sampled: in steep Aa reaches larval drift took place throughout the day, with little or no post-sunset peak, whereas in low-gradient Bb reaches, larvae were collected only during the first few hours after sunset (Iguchi & Mizuno, 1990). Moriyama et al. (1998) provided evidence that larval *R. brunneus* collected in Aa reaches in Japan had been entrained in plunge pools, eddies, and other

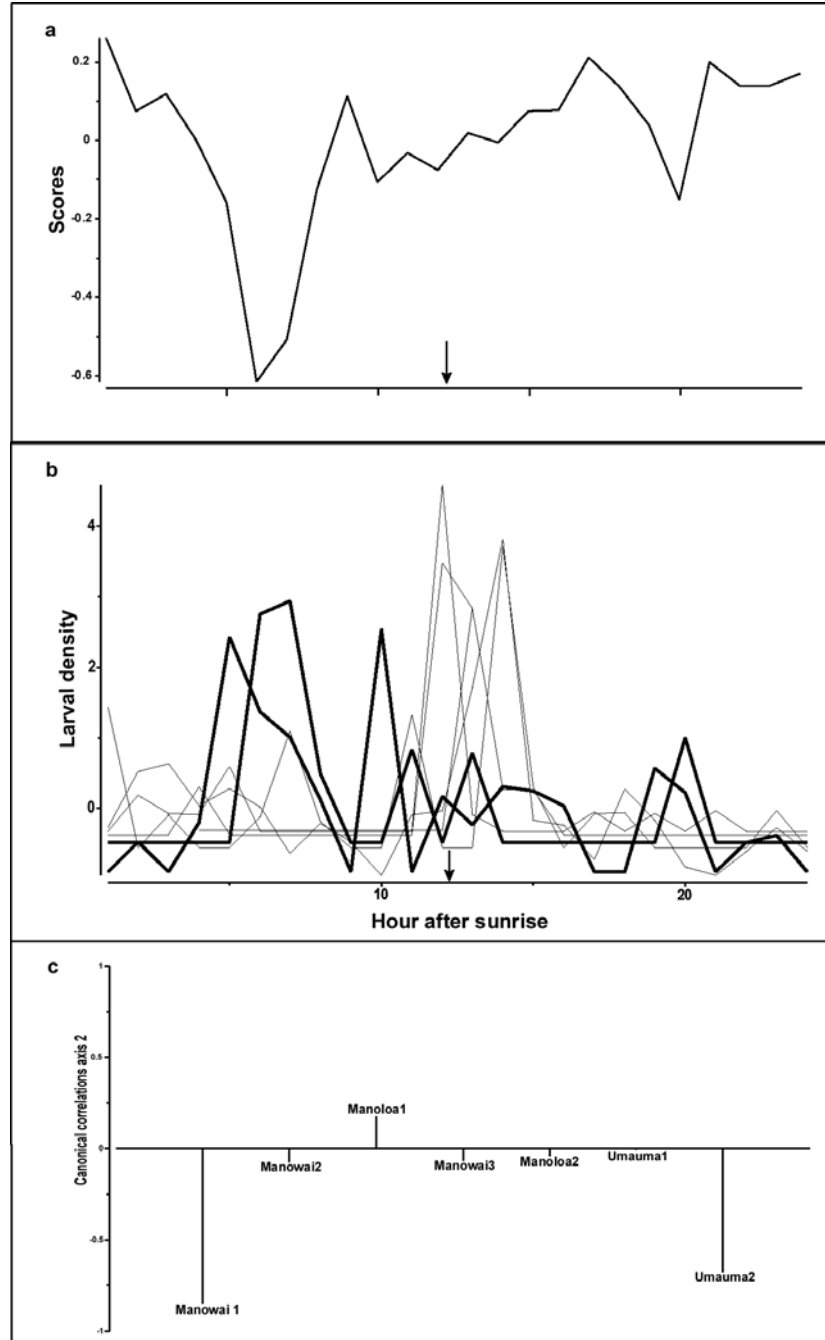


Figure 22. (a) MAFA axis 2, (b) the two 24-hour time series described by the common trend represented in MAFA axis 2, and (c) canonical correlations associated with each univariate time series with high loadings on MAFA axis 2. Position of black arrows on x-axis indicates sunset.

areas of turbulent flow which led to their capture in drift nets during the day and night. The steep, turbulent nature of the stream reaches sampled in the present study may similarly have contributed to the diel pattern indicated by MAFA axis; larvae may have been displaced from the main stream flow and entrained in eddies or side pools.

Although the trend indicated by the second MAFA axis was not statistically significant, this may be an artifact of the low number of time series ( $n = 7$ ) that were included in the analysis. Further research is needed to identify the mechanisms leading to the high degree of variability observed in the daily drift patterns for larval *L. concolor*. One hypothesis that could be tested in the future is that due to the abundance of turbulent stream features such as eddies and impounded plunge pools, *L. concolor* larvae are less able to control their downstream movements via vertical swimming than they are in less turbulent reaches. Another potential hypothesis to be addressed in future research is that the timing of hatching is related to the microhabitat characteristics of nest sites selected by adults. Lindstrom (1998) reported that hatching in captive spawned *L. concolor* could be induced at any time after 48 hours post-spawn by the mechanical disturbance associated with high water velocity. The daytime peaks in larval drift delineated by MAFA axis 2, therefore, may have been the result of larvae that hatched from nests located in microhabitats with high or variable water velocity, which could have resulted in “premature” hatching.

### **Lunar Periodicity**

No statistically significant lunar trends in the downstream drift of *L. concolor* larvae were indicated by the periodic regression performed on data combined from all sites sampled during this study (sites 1,2,3,5, and 6; Table 4). When analysis was stratified by reach type, however, a sinusoidal lunar cycle was evident ( $r^2 = 0.282$ ) in



samples collected near the mouths of the terminal waterfall streams (Figure 23, Table 4), even though periodic regression model fitted to the data did not indicate a statistically significant relationship ( $p = 0.137$ ). In terminal waterfall streams, larval densities were highest in samples collected during or immediately after a new moon (Figure 23). This observed pattern, although not statistically significant, was predicted *a priori* and corroborates observations of increased spawning activity during new moon phases in adult *L. concolor* raised in captivity (Lindstrom, 1998). By drifting to sea during the darkest nights, larvae may be better able to avoid predation by visually-oriented stream and marine fishes that feed heavily on prey items carried downstream.

The lack of significant lunar periodicity in larval drift in high elevation stream reaches that had large populations of adult *L. concolor* may be related to the high degree of variability in stream flow conditions that occurs in Hawaiian streams. Flash floods of extreme intensity frequently rise and fall in streams on the windward sides of the Hawaiian Islands (Tomlinson & de Carlo, 2003). The drift of unidentified goby larvae in Wainiha Stream on Kaua‘i decreased during the weeks following floods that were more than 4 times the baseflow discharge (Lindstrom, 1998). During the 2004 field season (February – May), at least three flood events that exceeded 4X baseflow were observed in Umauma and Hakalau Streams (see Figure 3) and may have been the factor that caused the observed lack of lunar periodicity in these streams. While flash floods are essential to the normal ecological functioning of Hawaii’s freshwater ecosystems (Fitzsimons et al., 1996), their occurrence, particularly in high-gradient stream reaches, may disrupt the complex territorial and courtship behavioral sequences that have been described in Hawaiian stream gobies, including *L. concolor* (Fitzsimons & Nishimoto, 1990).

Table 4. Coefficients and parameters of periodic regression models for analyses stratified by reach type.

Reach Type	$n$	$b_0$	$b_1$	$b_2$	$r^2$	$p$
Large-inland	59	0.328	-0.366	-0.091	0.081	0.113
Terminal waterfall	15	0.621	0.804	0.089	0.282	0.137
Terminal waterfall & Large-inland	74	0.290	-0.212	0.045	0.024	0.426

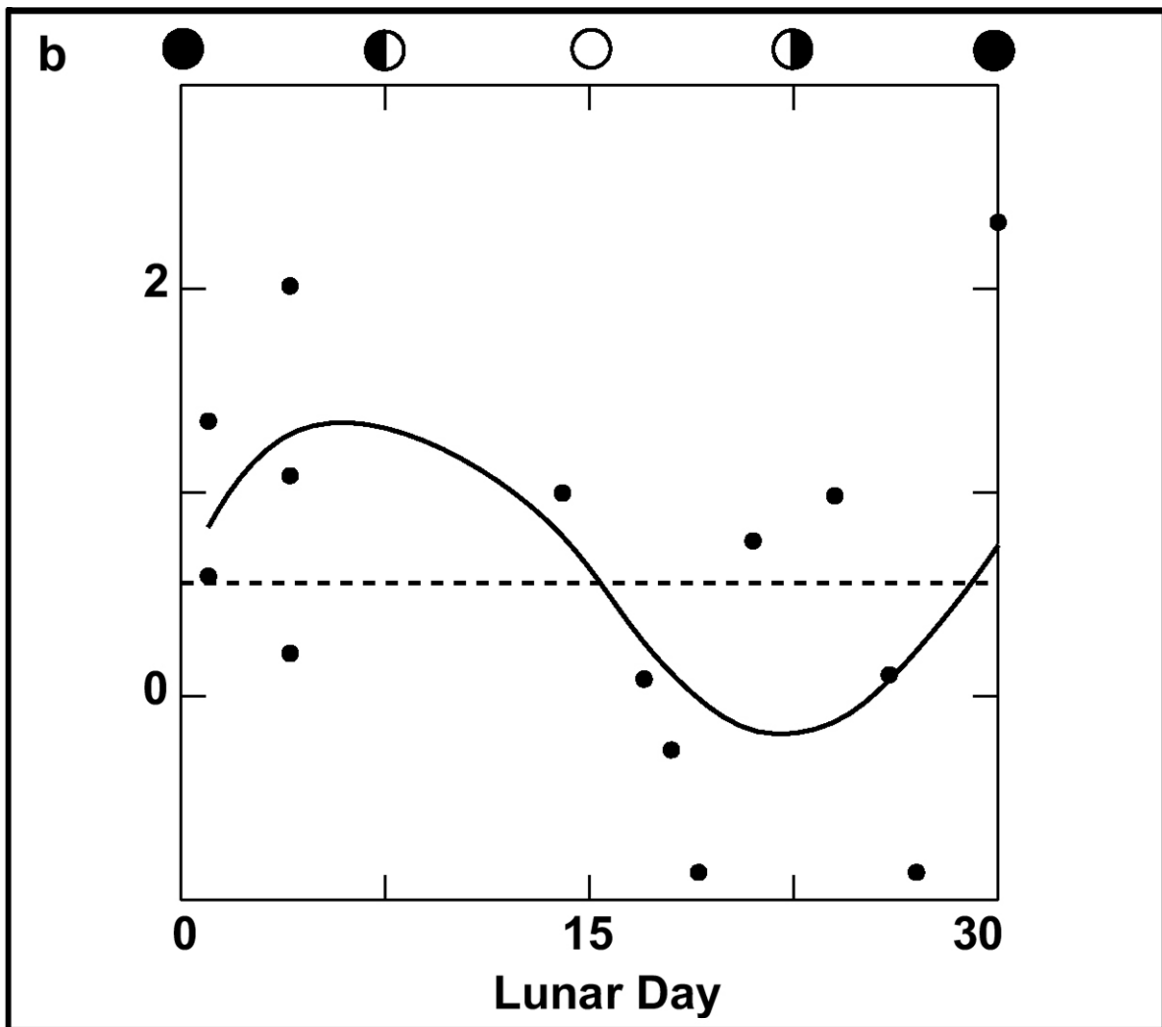


Figure 23. Lunar periodicity observed in *L. concolor* drift density observed in terminal-waterfall streams. Equation:  $y = 0.621 + 0.804 \cdot \sin \theta + 0.089 \cdot \cos \theta$  ( $r^2 = 0.282$ ,  $p = 0.137$ ).

Although benthic gobies are relatively well adapted to survive such events (Fitzsimons et al., 1997), some adult *L. concolor* and the substrates on which they build their nests are inevitably displaced downstream during the most intense freshets. By comparison, terminal-waterfall streams, because of their smaller catchment basins, are more stable environments. Even though flash floods do commonly occur in these smaller systems, they are typically less intense and therefore less likely to result in high mortality of adult *L. concolor* or in the destruction of their nests.

The research described in this chapter represents the first attempt to identify species-specific temporal patterns in larval drift of an amphidromous goby in Hawaiian streams. Drift of pre-marine *L. concolor* larvae took place during both day and night, with a statistically significant peak after sunset. Results also indicated that spawning activity in adult *L. concolor* may increase around the time of new moon phases, particularly in more stable habitats where they can consistently complete their complex territorial and courtship behaviors.

## **CHAPTER 4**

## **CONCLUSIONS**

## **Population Ecology**

The term “metapopulation” has been defined as a system of spatially separated local populations connected by dispersing individuals (Hanski, 1991). Kritzer and Sale (2004) defined the term metapopulation (as it applies to marine species) as "a system of discrete local populations, each of which determines its own internal dynamics to a large extent, but with a degree of identifiable and nontrivial demographic influence from other local populations through dispersal of individuals". The applicability of the term metapopulation to amphidromous fishes in Hawai‘i will be determined only through a more detailed understanding of how much exchange of offspring between different streams takes place. The populations of ‘o‘opu on all the Hawaiian Islands have been shown to be genetically similar and without island structuring (Chubb et al., 1998). If the larvae that recruit back to streams are originating from a truly panmictic pool of marine larvae, then the term metapopulation does not apply (Kritzer & Sale, 2004).

Recent studies have suggested, however, that mechanisms may exist that function to keep larvae from being advected away from their natal habitats (Ratdke et al., 2001; Sorensen & Hobson, 2005; Schoenfuss, pers. comm.). If so, there is a possibility that there may be substantial numbers of postlarvae that return to their natal streams, or to streams located nearby along the same coastline. This scenario would indicate that populations of Hawaiian stream fishes very likely fit the definition of true metapopulations.

For most species, habitats range widely in quality, and as such, habitat-specific demographic rates of local populations can have significant impacts on the growth and regulation of the overall metapopulation (Pulliam, 1988). “Sink” habitats have been defined as habitat patches (e.g., individual streams) where within-habitat reproduction is

insufficient to balance local mortality. Local populations in sink habitats can nonetheless persist through the input of continual immigration from more-productive “source” habitats. Source habitats are, in general, net exporters of individuals, while sinks are net importers of individuals (Pulliam, 1988).

Source and sink habitats are extremely difficult to identify (Watkinson & Sutherland, 1995). While results presented in this dissertation do not provide definitive evidence as to the identity of source and sink habitats for *Lentipes concolor*, they do suggest that for this species, and possibly for all of Hawaii's amphidromous fishes, some habitats are likely net exporters of individuals, while others are mainly net importers. The results presented in Chapter 2 provide the first evidence that the overall reproductive fitness of amphidromous gobies inhabiting Hawaii's various streams may be closely related to how far upstream they occur. Large numbers of larvae produced by a relatively small number of adult *L. concolor* in small nearshore reaches of terminal-waterfall streams consistently passed out of the stream mouth into the ocean. Conversely, larvae produced by large populations of *L. concolor* in the upper reaches of estuary streams were rarely observed to succeed in their seaward migration. The relatively high freshwater discharge produced by higher-order estuary streams, however, results in large freshwater plumes that extend into the nearshore marine environment. These plumes provide strong olfactory navigational cues for mass migrations of postlarval *L. concolor* as they make their return to fresh water and ultimately take up residence in mountainous stream reaches (Nishimoto & Kuamo‘o, 1997). Large streams with terminal estuaries, therefore, may very well be net importers of *L. concolor* (sink habitats), while small terminal-waterfall streams that likely attract relatively small numbers of postlarval recruits may function as net exporters (source habitats).

The results presented also highlight the possibility that source and sink habitats for *L. concolor* could exist in the same watershed. In large, higher-order streams, large numbers of offspring produced by a small number of adults that inhabit portions of the watershed at the downstream limit of their longitudinal distribution may consistently complete their seaward migrations. Conversely, larvae produced by much larger populations of adult *L. concolor* located farther upstream appear to consistently die while en route to the ocean. Given the frequent occurrence of high disturbance events in Hawaii's larger watersheds (e.g., flash floods) and the likelihood of high mortality in pre-marine and marine larvae, the long-term persistence of large populations of adult *L. concolor* in mountainous stream reaches may rely largely on the recruitment of individuals originally spawned either in nearshore reaches of the same watershed or in nearby terminal-waterfall streams.

When the population dynamics of Hawaii's other amphidromous fish species are considered in light of the results presented here, it becomes clear that a habitat functioning as a sink for one species could certainly be a source for another. Large streams with terminal estuaries may be playing a critical role as source habitats for the species of non-climbing 'o'opu (*Stenogobius hawaiiensis* and *Eleotris sandwicensis*) throughout the Hawaiian Islands. The low gradient, low water velocity habitats that are preferred by non-climbing 'o'opu are abundant in the long, sinuous terminal reaches of these streams, and these habitats are located close to stream mouths, where pre-marine larvae have easy access to marine habitats. The small, terminal-waterfall streams that appear to be so important for *L. concolor*, however, are almost assuredly ecological dead ends for postlarvae of the two non-climbing amphidromous fishes that may enter these streams only to encounter an unsurpassable waterfall a few meters upstream.



Although the results presented in this dissertation suggest that the upper reaches of large estuary streams in Hawai‘i may be sink habitats for *L. concolor* on an ecological time scale, it must be emphasized that these habitats have most likely served as refugia for this species at the evolutionary or geologic time scale. Volcanic activity creates new Hawaiian Islands at the southeastern end of the archipelago, while erosion leads to their eventual transformation into coral atolls at the northwestern end. One of the most dramatic erosional events that has occurred in the Hawaiian Islands has been the occurrence of catastrophic coastal landslides. Throughout Hawaii's geologic history, large coastal sections of the islands have broken away and collapsed into the ocean (Juvik et al., 1998). This process has undoubtedly impacted the geomorphology of Hawaiian Streams. Stream reaches that were once located in the headwaters of large watersheds with extended coastal reaches and estuaries (potential sink habitats for *L. concolor*) were likely transformed into short streams with terminal waterfalls. Short coastal streams (potential source habitats for *L. concolor*) that may have flowed through the portions of the islands that broke away would have been completely destroyed and could have, therefore, resulted in the extinction of local populations of adult *L. concolor*. In light of this long-term geologic instability of streams in Hawai‘i, the selective advantage incurred upon individuals that climb waterfalls and invade as far inland as possible becomes evident.

### **Conservation Implications**

Most fishes that live in continental streams and rivers are primary or secondary freshwater species that complete their entire life cycles within individual watersheds. As such, the fitness or health of individual populations in continental streams can be correlated with population size. Similarly, in these “closed” systems, it can be argued

that the population sizes of resident species and overall biological diversity are correlates of habitat quality. These relationships have led to the development of habitat assessment techniques that allow comparisons of the relative health (or biological integrity) of individual habitats based on the numbers of species and individuals present (Karr & Chu, 1999). Specific management plans can then be developed for individual habitats based on these assessments.

The unique aspects of the life-history strategies and population ecology of the indigenous fishes that live in Hawaii's streams and rivers necessitate unique approaches in the management of these species. The profound differences in the biological characteristics and ecological requirements that exist between adult fishes and newly hatched larvae result in there being no direct correlation between adult local population size and the ability of the individuals in that local population to reproduce successfully. A similar lack of a relationship therefore exists between local population density and habitat quality for these species (McDowall, 2000; Parham 2006). If a habitat is defined as an area in which a local population can successfully live and reproduce (i.e., produce successful offspring), then for Hawaiian amphidromous fishes, population size or density alone does not necessarily correspond to habitat quality. Thus, the applicability of habitat assessment techniques that incorporate correlations between population size or biodiversity and habitat quality is negated for Hawaiian stream ecosystems.

Habitat quality in individual streams must be assessed with regard to whether the habitat patch is a net exporter (source) or net importer (sink) of individuals (Parham, 2006). Such definitions of habitat quality depend on many variables including distance of reproducing individuals from the ocean, overall stream gradient between hatching sites and the ocean, water velocity-depth relationships between hatching sites and the ocean,

overall densities and distributions of predators downstream from hatching sites, *as well as* the local population density of adult ‘o‘opu that occupy that stream. When such variables are acknowledged as being critical measures of habitat quality in a stream, it becomes clear that densities of adult fishes in lower-quality, sink habitats may actually be greater at times than in the high-quality source habitats (Van Horne, 1983; Pulliam, 1988). If amphidromous fishes in Hawai‘i exist in open populations, then the scale at which habitat quality assessments should be made increases beyond the level of individual streams (Caley et al., 1996).

Patterns in the instream distributions of adult amphidromous fishes in Hawaiian streams are species-specific (Nishimoto & Kuamo‘o, 1991). Stream characteristics that define high-quality source habitats for one species (e.g., terminal waterfall streams for *L. concolor*) can define low-quality sink habitats for another species (e.g., terminal waterfall streams for *E. sandwicensis*). The number of species (i.e., biodiversity) of native amphidromous fishes in a single habitat patch (stream) is not, therefore, necessarily correlated to habitat quality. A stream that contains the entire compliment of Hawaii’s amphidromous fishes may only be a source for those species that live nearest to the mouth of the stream. For those species that live relatively far inland in these streams, recruitment into the habitat could far exceed successful seaward migration. Conversely, a stream could have only one species of fish present, and yet such a stream could export far more individuals of that one species than it imports.

Most anthropogenic perturbations in streams take place in lowland, nearshore reaches that lie between *L. concolor* hatching sites and the ocean. Such habitat alterations could negatively impact the species of ‘o‘opu that inhabit the affected reaches (e.g., *S. hawaiiensis* and *E. sandwicensis*), as well as species that may live farther upstream (e.g.,

*L. concolor*, *Sicyopterus stimpsoni*, and *Awaous guamensis*). Channelization or water extraction can alter stream morphologies and flow characteristics which could decrease the chances of successful seaward migration of the larvae of amphidromous species (Holmquist et al., 1998; Benstead et al., 1999; Concepcion & Nelson, 1999; March et al., 2003; Eikaas & McIntosh, 2006). The high densities of introduced larvivorous fishes that are abundant in altered or diverted stream reaches may be feeding on pre-marine 'o'opu. Human disturbances in lowland areas also lead to the elimination of near-ocean, high quality adult habitats for *L. concolor* while allowing upstream, inland populations to persist in undisturbed adult habitats in the same watershed. The high population densities of these species that exist in the inland reaches of such streams could actually be utilizing the lowest quality habitats present in that watershed because they might only rarely, if ever, have their offspring successfully migrate to sea.

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## VITA

Mark G. McRae was born on March 6, 1973 in Hilo, Hawai'i to Brenda and Robert McRae. From a very young age, Mark had a strong love of nature and the outdoors. He attended St. Joseph's Elementary and High Schools and graduated in 1991. His passion for the natural world inspired him to major in biology at the University of Hawai'i at Hilo where he remained for two years. After his second year at UH-Hilo, Mark transferred to Oregon State University and completed his bachelor's degree in wildlife science in March of 1996. After graduating from OSU, he continued to live in the Pacific Northwest and was employed as a stream surveyor which led to an intense interest in the ecology of streams and stream organisms. In August 1998, Mark moved to Baton Rouge, Louisiana to pursue his master's degree under the direction of Dr. J. Michael Fitzsimons. After completing his master's degree in December 2001, Mark began working towards obtaining his doctorate in biological sciences with Dr. Fitzsimons. After he defends his dissertation, Mark will continue studying the ecology of freshwater and estuarine organisms and will begin teaching at St. Petersburg College in St. Petersburg, Florida.